Petrodentine in Extant and Fossil Dipnoan Dentitions: Microstructure, Histogenesis and Growth

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Twelve characters are used to define petrodentine. The proposition that 'columns of petrodentine' are a late specialization in dipnoan tooth plates is examined.

Techniques of polarized light, microradiography and scanning electron microscopy are applied to consecutive sections and surfaces of the tooth plates, from which the microstructure of petrodentine is described. Its histogenesis and growth in both extant and fossil forms are also reported. Petrodentine is found in the tooth plates of *Neoceratodus* as well as *Protopterus* and *Lepidosiren* and in all fossil forms with tooth plates that have been examined, including the Middle Devonian *Dipterus valenciennesi* and the Late Devonian *Chirodipterus australis*. The arrangement of petrodentine within the whole tooth plate is considered to be an important character in dipnoans. Specialized cells in the dental pulp secrete petrodentine in phases of growth throughout the adult life. This secretion begins in the youngest denticles in the larval tooth plate. Because of this special development petrodentine is clearly different from the interdenteonal tissue of osteodentine.

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INTRODUCTION

Recent papers by Denison (1974) and Miles (1977) have challenged the statement that a pair of tooth plates on the prearticular and pterygoid bones is the primitive condition for dipnoans. Miles (1977) concluded from his investigation on the fossil dipnoans from the Gogo Formation of Western Australia that lungfish with tooth plates are a monophyletic group. He further stated that while tooth plates are a synapomorphy of higher dipnoans the primitive dentition comprises buccal denticles and tooth ridges. Miles proposed a rudimentary form of phylogenetic analysis as a cladogram (Miles, 1977: fig. 157) using a scheme attempting to order the origin of specializations within the group. One of the characters used as a specialization, developing late within those dipnoans with tooth plates, is the arrangement of the types of dentine into columns of petrodentine surrounded by trabecular dentine. This character is confined to the lepidosirenids.

The term petrodentine was proposed by Lison (1941) to describe one of the component tissues in the tooth plates of an extant lepidosirenid. This referred to the hypermineralized dentine developing in close proximity to trabecular dentine, but contrasting in the degree of mineralization. However, Ørvig (1976b) has compared dentine in other genera of dipnoans with petrodentine as defined by Lison (1941) and concluded that a type of hypermineralized dentine, with structural features equivalent to those in petrodentine, is present in forms as far back as the Devonian. Denison (1974) also described hypermineralized dentine, although he did not refer to it as petrodentine, in many other genera including the Devonian form *Dipterus fleischeri*. From these reports it was apparent that the tissue type 'petrodentine' needed to be

clearly defined, and that if equated with specialized hypermineralized dentine it was apparently more widespread amongst tooth plate-bearing dipnoans than was recognized by Miles (1977). It is clearly implicit in the statements of all three authors (Lison, 1941; Denison, 1974; and Ørvig, 1967) that a type of dentine can exist, within dipnoan tooth plates, in which the mineral content is considerably greater than normal dentine. A comparable tissue with a high percentage of mineral and a low percentage of organic matrix, derived by modification of dentine matrix, is the enameloid cap in the teeth of elasmobranchs and teleosts (Smith, 1980). However, the arrangement of petrodentine within the tooth plate and its histogenesis throughout ontogeny imply that it is a special type of dentine with clearly defined characters different from enameloid. Published accounts make it difficult to establish what these characters are and, therefore, difficult to compare the tooth plate structure of both fossil and extant genera.

With these objectives I have attempted to derive a set of criteria to characterize the tissue type petrodentine as first described in *Protopterus aethiopicus* Owen (Lison, 1941). This has involved a critical survey of the literature and new observations on both extant and fossil dipnoan tooth plates. The current study is concerned with three aspects of hypermineralized dentine in dipnoan dentitions. These are 1) the arrangement, microstructure and growth of petrodentine in tooth plates of extant forms; 2) the characters used to identify petrodentine from observations in polarized light, microradiography, and scanning electron microscopy; and 3) an analysis of the distribution of petrodentine amongst forms with tooth plates throughout the fossil record.

Information on the structure of tooth plates, their component tissues and their pattern of growth is of no value in assessing relationships between dipnoans, tetrapods and crossopterygians if it is accepted that tooth plates are a synapomorphy of higher dipnoans. However, it is of some value to establish characters of the dentition in any consideration of dipnoan interrelationships and in any study which seeks to distinguish primitive from derived characters of dipnoans as a prelude to recognizing characters synapomorphous with tetrapods or crossopterygians.

CRITICAL REVIEW AND TERMINOLOGY

The tissue in dipnoan tooth plates called 'petrodentine' (Lison, 1941) was first described by Owen (1839) in *Protopterus annectens* Owen as 'clear substance' because of its obvious translucence relative to dentine and bone. Prior to the suggestion by Lison (1941) that a new term should be used for this special category of dentine, both Kerr (1903) and Nielsen (1932) acknowledged that it is characterized by extreme hardness. They termed it vitrodentine and enamel respectively. Subsequent to those accounts Ørvig (1967) and Schmidt and Keil (1971) have discussed the structural similarity of the tissue in dipnoan tooth plates with durodentine (synonymous with enameloid, Poole, 1967) in elasmobranch and actinopterygian teeth, although they correctly recognized that histogenesis of this tissue is different in dipnoans from that of enameloid. All these terms are based on the composition of only one of the structural components of the tooth plate and its properties of hardness and translucency. Other terms for the dental tissues are derived from the composite arrangement of the hard and soft tissue components; these are syndentine (Thomasset, 1928, 1930), tubular dentine (Nielsen, 1932; Moy-Thomas, 1939), pseudohaversian osteodentine (Lison, 1941), compact or vascular pleromin (Ørvig, 1976b), trabecular dentine (Denison, 1974), central columnar dentine (Kemp, 1979).

The term tubular dentine is based on the parallel arrangement of vascular canals running through the tooth plate from the formative surface to the tritural surface. Denison (1974) used this term in his general review of the structure of teeth in

lungfishes, believing that this regular arrangement of vascular canals was derived from the primitive type of trabecular dentine, with irregular vascular canals, as a specialization. The difficulty of using this term has been previously discussed (Radinsky, 1961; Smith, 1979a). The term syndentine (Thomasset, 1930) is another one based on overall structure, implying that it is derived in ontogeny from separate parts now joined together. This is not a feature that could be recognized in the mature tissue and most subsequent workers have rejected the term (Smith, 1977). Denison's concept of the tissues in lungfish tooth plates is slightly ambiguous. He stated that both trabecular dentine, found in many of the tooth plates, and tubular dentine are highly mineralized. However, Denison (1974) chose to recognize as petrodentine only the hypermineralized dentine arranged as columns as in the lepidosirenids. Nowhere does he state that all the examples of hypermineralized dentine may be equivalent to petrodentine. As it is one of the objectives of this paper to consider the evidence for the distribution of highly mineralized dentine (petrodentine) within tooth plates of dip-noans, Denison's observations will be included in the next section.

Ørvig (1951) in a comprehensive study of tissues in placoderms and elasmobranchs recognized that 'tubular dentine' is a distinctive tissue, different from trabecular dentine (osteodentine) found extensively in teeth of fishes. He reached this conclusion because he regarded 'tubular dentine' as having a different ontogenetic pathway and, more importantly, a different structure. The main reason for this statement is the different cellular origin of the interstitial tissue, although Ørvig (1951) regarded the tubular component as analogous with dentinal osteons of osteodentine. Lison (1941) was faced with the same difficulty of a general terminology for the tissue around the petrodentine in the whole tooth plate. He called it 'pseudohaversian osteodentine'. This is an unnecessarily complicated term because once it is accepted that the component of dentine arranged in concentric layers around the vascular canal can be compared with an osteon (denteon), then by analogy with compact bone the denteons can form either with or without prior resorption of the interstitial tissue. In both cases the denteons compare with the true Haversian systems, both primary and secondary ones. Many different categories of osteodentine are illustrated by Ørvig (1951: figs 1, 2) and again his term osteodentine (Ørvig, 1967: 102) includes all dentines which start as trabecules of mineralized tissue (woven-fibred, coarse-bundled) and become compact by growth around the blood vessels of concentric dentine layers (denteons). In this category he included as osteodentine the tissue at the margins of the tritural columns in holocephalan and dipnoan tooth plates. Again, Ørvig had accepted that the columnar tissue forming the wear-resistant ridges (triturators) of the tooth plate is different from any of the other osteodentines. In his 1967 review Ørvig decided to recognize a new category, columnar pleromic hard tissue, for these hyper-mineralized tissues forming initially in a superficial position and growing continuously in a basal direction.

Essentially this pleromic hard tissue, or pleromin, is the main component of the ridges of the tooth plate and is equivalent to petrodentine. I reach this conclusion because Ørvig still felt it necessary to have two terms for the different composite tissues. Where the composite tissue is formed of tritural columns of pleromin separated by parallel denteons, he referred to it as vascular pleromin and still rejected the term 'tubular dentine'. Hence Ørvig (1976a,b) proposed the recognition of two types of pleromic hard tissue: vascular pleromin (synonymous with tubular dentine) typified by the tissue in *Neoceratodus* and *Ceratodus,* and compact pleromin, blocks or columns of petrodentine without vascular canals except at the margins of the tritural column, typified by *Monongahela* and *Lepidosiren.* Kemp (1979) rejected all previous terms and referred to 'central columnar dentine' in toothplates of *Neoceratodus forsteri.*

By this stage of the review we have identified the main problem, that is, are Denison (1974) and Miles (1977) correct in considering the most significant features of the tooth plates to be the arrangement of the component tissues, i.e. columns of petrodentine with or without vascular canals, or should emphasis be primarily on whether there is a special histological type of dentine that is hypermineralized and of continuous growth from the basal surface? Some conflict of opinion can be found in Denison's (1974) account because, as Miles (1977) observed, he described the tooth plates of *Monongahela,* a gnathorhizid, as showing a distinctive histological structure comparable with that of *Protopterus,* while those of *Gnathorhiza,* were claimed to be sufficiently different not to support a close relationship with lepidosirenids.

Most people searching for homologies in the tissues have been faced with this plethora of names and been unable to reach agreement. Ørvig (1951, 1967, 1976a,b) recognized the special type of dentine in dipnoans (and holocephalans), principally for two reasons — it is extremely hard and lacks collagenous matrix, and it grows continuously at the basal surface by elongation into the tissues supporting the tooth plate. After consideration of all the possibilities for a comparison between dipnoan tissues and osteodentine in general, we are left with the statement that the interstitial tissue between the denteon systems in dipnoan tooth plates is different in its development, structure and growth from the 'inter-denteonal' tissue of osteodentine. It is this statement that we must examine.

If we accept that tooth plates are a specialization in dipnoan dentitions (Denison, 1974) and that they evolved only once (Miles, 1977), then petrodentine would be an additional specialization confined only to those forms with tooth plates. It is also apparent that we must decide whether or not it is another specialization to have the petrodentine arranged into columns (compact pleromin) or interspersed with regularly arranged vascular canals (vascular pleromin). Ørvig (1976b) also claimed that the pleromin of holocephalan tooth plates is arranged in columns in some forms, although he noted that it differed from that in *Lepidosiren* in a detail of the histological structure (Ørvig, 1983). It is implicit in both Denison's (1974) and Miles's (1977) statements that arrangement into columns of petrodentine is the significant advanced character. If this is in fact so then we must look for the pattern in the distribution of these tissues amongst the genera of dipnoans.

REVIEW OF THE DISTRIBUTION OF PETRODENTINE WITHIN DIPNOANS

Characters of the tissue

It is quite clear from the literature that all dipnoan tissues described by Ørvig (1967, 1976a,b) as pleromin have the properties of the tissue first described by Lison (1941) as petrodentine. In the review of dental tissues by Schmidt and Keil (1971) they equated the petrodentine with durodentine (enameloid, Poole, 1967) of elasmobranchs and actinopterygians, although Schmidt and Keil (1971) noted that the petrodentine forms out of contact with the dental epithelial cells, and is therefore, quite different from enameloid. Ørvig (1967a,b) had recognized that a special population of cells, pleromoblasts, is responsible for the production of pleromin in all groups that he studied and that this method of histogenesis is a significant difference from that of enameloid. Lison (1941) had originally also described two populations of cells developing within the pulp cavity — petroblasts secreting petrodentine and odontoblasts the dentine. All the characters that may be used to describe the tissue petrodentine are listed in Table 1. The important ones to distinguish it from enameloid are numbers 10 and 11; both are difficult but not impossible to demonstrate in fossil material. In many adult tooth plates new material, in the form of denticles, is added at the labial margins and these provide examples of tissue histogenesis as in earlier on-

TABLE 1

Characters used to identify petrodentine in extant and fossil tissues *

1. not diagenic, not stained during fossilization
2. translucent in transmitted, non-polarized light
3. few tubules, or if present, very thin and confined to margins
4. hypermineralized relative to normal dentine and bone
5. birefringence due to mineral component, bands crossed at right angles
6. opposite signs of birefringence in adjacent regions; each band inclined 45° to the vertical axis
7. assumed formation from fibre-based matrix, with crystals in groups retaining the fibre orientation
8. continuation of crystal-fibre bundles with collagen-fibre bundles at margins
9. extreme reduction of organic matrix, concomitant with mineralization
10. continuous sequential growth at abtritural surface from pulpal cells
11. develops late in histogenesis of the tissues in each denticle or region
12. forms in earliest ontogenetic stage of the tooth plate

* compiled from publications by Lison (1941), Ørvig (1967, 1976), Schmidt and Keil (1971), Smith (1980).

togenetic stages. In the denticles at the labial margins of the tooth plates of *Sagenodus inaequalis* (Smith, 1979), petrodentine develops later than the peripheral dentine (Table 1 — character 11). Identification of forming surfaces roofing a pulp chamber, and sequences of growth lines parallel to this surface in many fossil genera show that growth is continuous and extensive (Table 1 — character 10). The pattern of growth in dipnoan tooth plates has been investigated by new methods (Smith, Boyde and Reid, 1984) and an analysis of this is in progress (Smith, MS).

Extant genera

The translucency, lack of tubules and non-diagenic properties of petrodentine (Table 1 — characters 1-3) were the only characters referred to by the early workers; both Schmidt and Keil (1971) and Ørvig (1976) cite these references. The first description of the histology of any tooth plate was by Owen (1839, 1841, 'clear substance') in *Protopterus annectens* and also in *Lepidosiren paradoxa* (Owen, 1845: 159, fig. 4). Günther (1871) first described the 'clear substance' between the vascular canals in *Neoceratodus forsteri*.

In the larval stages of the extant forms Parker (1892) noted what he called 'infilling dentine' in *Protopterus aethiopicus*, later used by Jarvik (1967) as an example of pleromin (Ørvig, 1967). Ørvig (1967: figs 45a,45b) figured Lison's findings as examples of the ontogenetic development of pleromin. Kerr (1903) described the dentine in this position in *Lepidosiren paradoxa* as vitrodentine (after Röse, 1892). Semon (1899) studied the early stages of *Neoceratodus forsteri* and described intrapulpal dentine in the position of the infilling dentine of Parker (1892). The account of tooth plate development in larval stages of *Protopterus aethiopicus* by Lison (1941) clearly demonstrates that this infilling dentine is petrodentine in the early ontogenetic stages (Table 1 — character 12). An account of the growth of petrodentine in larval stages of *Protopterus aethiopicus* by Smith (1984) shows how continuous extensive growth of petrodentine contributes to the structure of the larval tooth plate. Both these studies show that petrodentine is secreted from pulpal cells after a cone of primary dentine is formed (Table 1 — character 11). Similarly, recent studies on *Neoceratodus forsteri* (Kemp, 1979) show that petrodentine (central columnar dentine) starts to form from pulpal cells within the primary dentine and that continuous growth from this surface contributes to the main tissue mass of the tooth plate.

Lison (1941) figured the adult tooth plates of *Protopterus aethiopicus* with the

translucent columns of petrodentine without tubules contrasting with the dentine with tubules surrounding the vascular canals. Growth lines are not mentioned although he did suggest that growth is continuous from special pulp cells (Table 1 — character 10) and that a differential rate of growth allows the vascular canals to be included at the margins of the petrodentine. Lison concluded that it is exactly the same tissue between the vascular canals of *Neoceratodus forsteri*. Schmidt and Keil (1971) described the polarized light appearance of petrodentine of *Protopterus aethiopicus* and concluded that the bands crossing at right-angles are due to crystals following the course of the collagen fibres. These crystal-fibre bundles are continuous with the collagen fibres of the dentine (Table 1 — characters 5, 7, 8) and at the junction between the two tissues there is a neutral, or apparent isotropic zone. In a study of the growth of tooth plates in *Protopterus annectens* (Smith, 1984) it is shown that petrodentine is added to the abtritural surface and that this increases in extent not only at the labial and posterior margins but also at the lingual or palatal margins (Table 1 — character 10). Also demonstrated are the lines of low mineral density, in sequence and parallel to the formative surface; these are interpreted as lines of growth.

A section through a tooth plate of *Lepidosiren paradoxa* is figured by Tomes (1904) showing apparent superimposed layers of the petrodentine (translucent material). Denison (1974: fig. 14) illustrated a similar section through the tooth plate of *Lepidosiren paradoxa* and described the same region as hypermineralized, also showing growth lines, although these were not described. Scanning electron micrographs of *Lepidosiren* sp. from the Upper Miocene are figured by Ørvig (1976b: figs 22-25) and these show the distinctive microstructure of woven crystal-fibre bundles between the vascular canals.

Ørvig (1976b: figs 13, 14) figured Günther's illustrations of *Neoceratodus forsteri* and referred to the petrodentine (pleromin) as the tissue between the vascular canals, as Lison (1941) had also previously concluded. He also illustrated, in horizontal sections (Ørvig, 1976b: fig. 19), the typical birefringence of the petrodentine and the characteristic microstructure in polarized light, of radial bundles around the vascular canals. This is contrasted with osteodentine in which there is no hypermineralized interstitial matrix, formed of radially oriented crystal-fibre bundles between the denteons (see Ørvig, 1951). The ultrastructure of petrodentine in ceratodontids is shown by Ørvig (1976b: figs 15, 16) in a Triassic genus and, as in lepidosirenids, this shows the crystal-fibre images of coarse intertwining fibre bundles. Kemp (1979), referring to this part of the tissue as central material, decided that it had not formed following the loss of a collagen fibre matrix as it first appears with only scant reticulin fibres, but she offered no alternative explanation of the basis for the crystal-fibre bundle images. As I have also concluded (Smith, 1980) the basis for the orientation of the crystallites is not established. It could be determined by the matrix or by the cell processes at the formative front.

The fact that petrodentine is hypermineralized has been assumed from its translucency, hardness and appearance in acid-etched scanning electron micrographs. The degree and extent of this hypermineralization has only recently been demonstrated using microradiographic information (Smith, 1980, 1984). From these studies it is apparent that the degree of mineralization is very high indeed, of the same order as enamel in the teeth of tetrapods, and enameloid in elasmobranchs and actinopterygians (Table 1 — character 4). Preliminary studies on quantitation of microradiographs show that petrodentine is 4½ times as dense as dentine. This compares with human enamel which is 5 times as dense as dentine. This is true of all three extant genera of dipnoans. The reduction of the organic matrix with progressive mineralization of the tissue has been shown by Lison (1941) and James (1957), (Table 1 — character 9).

The arrangement of the hypermineralized dentine in *Protopterus* and *Lepidosiren* is described by Denison (1974) as alternating columns of petrodentine and trabecular dentine. Ørvig (1976b) termed this compact pleromin. Both regarded such tissue as an advance on the type called hypermineralized trabecular dentine (Denison, 1974) or vascular pleromin (Ørvig, 1976b). Compact pleromin is the advanced character in dipnoan tooth plates referred to by Miles (1977b) as 'columns of petrodentine'. Although, as Ørvig (1976b) stated, in all forms the tissue starts off as compact pleromin in the larval tooth plates.

Fossil genera

Petrodentine is a major part of the tritural columns of the ridges of the tooth plate in *Lepidosiren* sp. from the Miocene (Ørvig, 1976b). Günther (1871) figured sections of *Ceratodus runcinatus* Pleininger, a Triassic form showing petrodentine between the vascular canals, which he compared with *Neoceratodus forsteri*. He also showed growth lines parallel to the tritural surface; a sequence of growth lines is also figured by Stromer and Peyer (1917) and the ultrastructure of these lines is recorded by Smith, Boyde and Reid (1984). Schmidt and Keil (1971) concluded that the histological features of *Ceratodus kaupi* Agassiz, another Triassic ceratodontid, are similar to those of *Protopterus*. They recorded the non-diagenic, unstained character (Table 1 — character 1) of the tissue between the vascular canals and contrasted this with the dentine surrounding the canals (Schmidt and Keil, 1971: fig. 181). The other features noted by them are a matted feltwork of fine tubules, and a pattern of birefringence, typical of petrodentine, in which the birefringent fibre bundles are organized radially adjacent to the vascular canals. Ørvig (1976b: figs 15, 16, 17) has also produced scanning electron micrographs of this tissue, clearly petrodentine, in a Triassic ceratodontid. Stromer and Peyer (1917) figured sections of *Ceratodus parvus* Agassiz from the Upper Triassic and these show that the organization of petrodentine is such that it is beneath each crest of the ridges in these radiate tooth plates. Denison (1974: fig. 8) illustrated a section through two denticles of a juvenile tooth plate of *Ceratodus parvus* and commented that this tissue is unspecialized, highly mineralized, trabecular dentine.

Since these early reports, only Denison (1974) and Ørvig (1976b) have commented further on the types of dentine in fossil dipnoan tooth plates and they have produced conflicting opinions on the significance of the distribution of petrodentine amongst these groups. It is apparent that all forms assigned to the families Lepidosirenidae and Ceratodontidae possess petrodentine as a major component of the tooth plate. In the former group it is arranged as columns (compact pleromin; Ørvig, 1976b) and in the latter petrodentine is frequently interspersed amongst parallel vascular canals (vascular pleromin; Ørvig, 1976b). The proportion and arrangement of trabecular dentine (osteodentine) at the margins of the petrodentine varies considerably amongst the genera, and it may be that this feature is as significant as the presence or absence of petrodentine. The morphology of the tritural surface of the tooth plate is affected by the distribution of petrodentine and trabecular dentine, with their inherently different rates of wear. This variation is shown by Tabaste (1963) in the Lower Cretaceous ceratodontids in sections of *Ceratodus tuberculatus* Tabaste and *Ceratodus africanus* Tabaste. Schultze (1981) compared the histology of flat-surfaced Lower Cretaceous tooth plates of *Ceratodus frazieri* Ostrom with that of *Ceratodus africanus* and described patches of osteodentine (trabecular dentine) between large areas of petrodentine. These patches of osteodentine were observed to correspond with the circular depressed areas on the tritural surface.

Amongst the genera of dipnoans possessing radiate tooth plates (Denison, 1974), there are only a few in which the histology has been investigated. Denison (1974: fig.
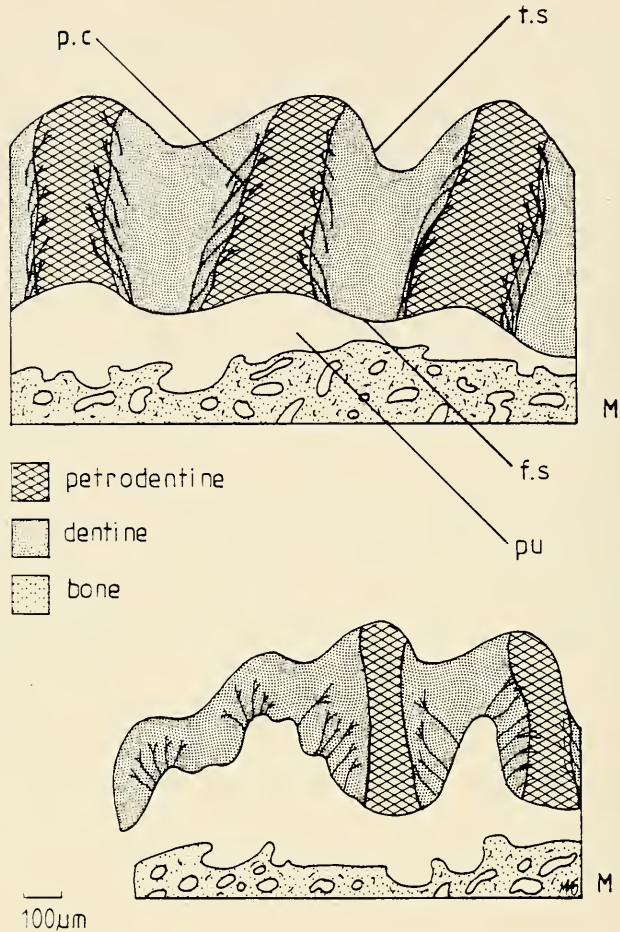
Fig. 1. *Monongahela dunkardensis* Lund. Juvenile tooth plate, vertical sections along one ridge (Prev. figs 12 & 13, Denison, 1974; F.M. 5507, 5505). Regions of petrodentine separated by dentine. Pulp canals terminating in dentine tubules pass across the border between tissues. Labial margin of tooth plate, no petrodentine in youngest denticles. Key to this figure is the same for all subsequent drawings (see p.407).

12) described young tooth plates of *Monongahela dunkardensis* Lund, an example of a Permian form, and illustrated the arrangement of columns of hypermineralized dentine (petrodentine), alternating with trabecular dentine. Ørvig (1976b) later referred to this as compact pleromin. I was fortunate to be able to examine the same section (Field Museum 5502) in polarized light and found that the column of translucent dentine showed alternating signs of birefringence either side of an isotropic zone (Table 1 — character 6). This together with other features confirmed my opinion that there is petrodentine in this genus. I was also able to observe in a section through the youngest tissue at the labial margin of one ridge (Fig. 1), that these columns of petrodentine develop late in the histogenesis of each denticle of the tooth plate.

The tooth plates of *Gnathorhiza serrata* Cope were described as consisting of ordinary trabecular dentine (Denison, 1974: fig. 15). However, examination of the same section in polarized light convinced me that part of this tissue is petrodentine. Of the

Carboniferous forms, Denison (1974) described the tooth plate of *Sagenodus* sp. as a thick layer of highly mineralized 'tubular dentine' (vascular pleromin of Ørvig, 1976a,b) and commented that the newest denticles at the labial margin show how this tissue was initially formed. The growth of the tooth plates of *Sagenodus inaequalis* was studied (Smith, 1979) and this confirmed Denison's observations that growth is continuous beneath the tritural surface and areal growth is by extension at the labial margins. It was concluded that the major part of the tooth plate is petrodentine and that this forms late in histogenesis of the newly-added denticles.

Devonian dipnoan genera are of the greatest importance in determining the stratigraphic record of the distribution of petrodentine. Denison (1974) has stated that the specialized dentine (tubular dentine/vascular pleromin) only occurs in post-Devonian dipnoans. However, on this point, Denison also states that both the simple trabecular dentine and the tubular dentine are highly mineralized. So, once again, we find that statements are made about the interstitial component being hypermineralized but the arrangement of vascular canals is either irregular and branched, or regular and parallel. Ørvig (1967) has used the embracing term pleromin for both categories, but Denison (1974) and Smith (1979a) rejected this usage. However, Ørvig is almost certainly correct in assuming that a special kind of hypermineralized dentine (petrodentine) forms in many of the genera of Devonian dipnoans, and he gives *Scaumenacia* and *Rhinodipterus* as examples. (Examination of Ørvig's material, generously made available to me, both s.e.m.'s and slides, confirmed that this is a valid conclusion.) Denison (1974) also decided that the dentine in *Scaumenacia* is highly mineralized, because of the translucency and relative lack of odontoblast tubules. (I have examined the section figured by Denison (1974: fig. 5) but it is very difficult to interpret because the mounting medium has begun to crystallize.) Of the other Devonian dipnoans examined by Denison, a section of *Dipterus valenciennesi* is illustrated in which patches of hypermineralized dentine are in the centre of each denticle cusp, (Denison, 1974: figs 2,4) but this is regarded as pleromic dentine *sensu* Tarlo and Tarlo (1961) (for discussion see Smith, 1977). Smith (1977: figs 70,71) figured the tooth plates of the Late Devonian *Chirodipterus australis* but she made no decision about the type of dentine forming the interstitial tissue between the vascular canals.

From this review of the literature it is immediately apparent that there has been little agreement, either on the type of dentine or its mode of growth in Devonian forms. However, as a basis for further investigation, the general statement can be made that a type of hypermineralized dentine, petrodentine, probably occurs in a variety of Devonian dipnoans with radiate tooth plates.

There are still divergent views on the primitive condition of the dentition in dipnoans and the statements made by Denison (1974) and Miles (1977) that tooth plates are a derived character has been challenged by Campbell and Barwick (1983). They have stated that amongst early Devonian dipnoans there were already two different types of dentition, crushing plates of dentine on the pterygoid and prearticular as in *Dipnorhyncus sussmilchi* Etheridge and *Speonesydrion iani* Campbell and Barwick and a shagreen of small denticles with marginal dentine ridges as in *Uranolophus wyomingensis* Denison. They have argued that Denison (1974) did not define the term tooth plate precisely and the exclusion of *Dipnorhynchus* from the tooth plate-bearing group is not justified. Prior to the statements made by Denison (1974) the view that *Dipnorhynchus* represented the primitive condition was widely accepted (White, 1965; Thomson, 1967). If petrodentine is regarded as a feature of tooth plates, and *Dipnorhynchus* and *Speonesydrion* are accepted as members of the group with tooth plates, it becomes important to establish if they have petrodentine in the dental tissues. Moreover, the

examination of the dental tissues in early denticulated genera such as *Uranolophus* and *Griphognathus* for petrodentine also becomes of some importance.

Material-Techniques

MATERIAL

Protopterus aethiopicus Owen

Serial, coronal sections through larval stages of 27.5 mm, 54 mm and 57 mm. BM(NH) P10362-P10839.

S.e.m. blocks as cut, polished and etched surfaces; either 0.1NHCl for 1 min. or 1NHCl 10-30 sec., S45, S46: Consecutive ground sections, vertical labio-lingual, M47: Lower jaw segment RCS/OM-A449.3.

Decalcified serial sections, vertical labio-palatal, through upper tooth plate, stained H & E, Mallory, Masson, WJ 5/49.

Lepidosiren paradoxa Natterer

S.e.m. blocks as cut, polished and etched surfaces; 0.1NHCl for 1 min, 10 min 10% NaOCl, Critical point dried, S65, 66, 67: Consecutive ground sections M65: Lower jaw segment from specimen supplied by Dr N. A. Lockett from the 1977 Amazon ∝ Helix Research Expedition.

Lepidosiren sp.

Upper tooth plate, Miocene, La Venta Formation, Colombia, South America; collected by Dr Kubet Luchterhand, on loan from the Field Museum of Natural History, Chicago. PF9005.

Protopterus sp.

Upper tooth plate, Eocene, Mali, Africa; collected by Ms Alison Longbottom, joint expedition 1981 BM(NH) and Kingston Polytechnic, Dr Cyril Walker.

Neoceratodus forsteri Krefft

Decalcified, vertical sections through upper tooth plate, H & E, Alcian Blue & Safranin, BM(NH) 5005, 5006. S.e.m. blocks (prepared as *Protopterus*) S41-44: Consecutive ground sections vertical and horizontal M41-43. Specimen from Warwick James Collection, Royal Dental Hospital.

Ceratodus madagascariensis Priem

Upper Cretaceous, NW Madagascar, upper tooth plate, vertical, ground sections, BM(NH) P15660.

Ceratodus runcinatus Pleininger

Triassic, Lettenkohle, locality Hohenech; upper right tooth plate vertical ground sections and s.e.m. block S137, S139 from specimen PV 19270; s.e.m. block S145 from specimen PV 19279.

Ceratodus kaupi Agassiz

Triassic, Lettenkohle, locality Bibersfeld; lower right tooth plate vertical ground sections and s.e.m. block S140 from specimen PV 4460.

Sagenodus inaequalis Owen

Carboniferous, Coal Measures, Northumberland; upper tooth plate, vertical ground sections, BM(NH) P7326, P3381.

Dipterus valenciennesi Sedgwick and Murchison

Middle Devonian, Caithness; upper tooth plates, vertical and horizontal ground sections through specimens BM(NH) P 44671, P 53537.

Chirodipterus australis Miles

Middle Devonian, Gogo, Australia; vertical labio-lingual section and consecutive s.e.m. blocks, through upper and lower tooth plates; BMR 22592-4, BM(NH) P 52561.

TECHNIQUES

Photomicrographs

Ordinary light, polarized light and phase contrast, Zeiss Photomicroscope III; Camera Lucida drawings on Zeiss Universal.

Microradiographs

X-ray generator, Phillips PW 1720, copper anode, fine focus 300μm beryllium window; PW 2213/20. Kodak high-resolution spectroscopic plates 649-0; 30kV 33mA, 10 mins.

Scanning electron micrographs

SE-mode, Cambridge Mark 2A, operated at 30kV; Coates and Welter Kwikscan, field emission cathode, operated at 15kV; St. George's Hospital Medical School. Cambridge Stereoscan 180, operated at 30kV, Electron Microscopy Unit, ANU. BSE-mode, Cambridge Stereoscan S4-10, operated at 20kV, Hard Tissue Unit, Anatomy Department, University College, London.

OBSERVATIONS

The histology and microstructure of the dental tissues of the extant genera and several fossil genera have been investigated using the four techniques previously described by Smith (1979b, 1980) and Smith, Boyde and Reid (1984). The methods which use ground sections, decalcified sections and blocks of tissue, some made anorganic by the removal of cells and organic matrix, are:

 i) the level of hypermineralization by microradiographic analysis;
 ii) optical properties by polarized light;
 iii) the ultrastructure by s.e.m. of polished and etched surfaces, or anorganic surfaces;
 iv) histogenesis by comparison of mature regions with forming surfaces in all types of preparation.

The terminology of Smith (1979), which Schultze (1981) also adopted, will be used. Where the vascular canals ascend in the direction of the tritural surface they will be called pulp canals. Gross (1956) described the narrow branching tubes running through the dental tissues of *Dipterus* and *Rhinodipterus* as pulp canals (Fig. 2). This
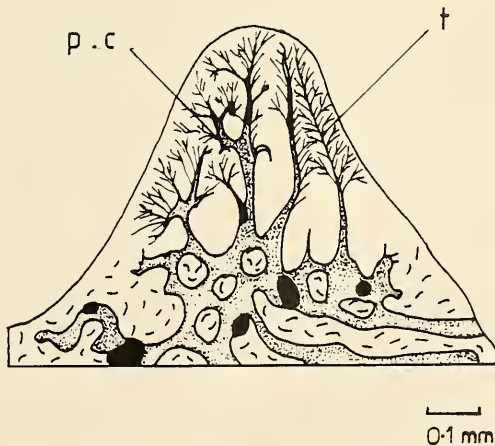
Fig. 2. *Rhinodipterus secans* Gross. Drawing from Gross (1956: fig. 122B). Vertical section through one denticle of the tooth plate. Pulp canals run into the dentine from the tissue spaces in the bone, finer tubules penetrate the dentine from the pulp canals.

seems entirely justified as many fine tubules, housing the odontoblast cell processes, lead out of the pulp canals and permeate the dentine in the adjacent region. Where the dentine surrounding the pulp canals is clearly a distinct tissue on the basis of its fibre organization, level of mineralization and content of tubules, it is termed circumpulpal dentine.

The observations that follow attempt to show in each form, both extant and fossil, as many of the characters of petrodentine as possible within the limits of the available material. The characters used are those given in Table 1.

1. *PROTOPTERUS AETHIOPICUS* — **Larval**

Detailed aspects of the growth of tooth plates in larval stages are discussed by Smith (1984). Sufficient additional information is given here to comment on the ontogenetic development of petrodentine in the early development of the dipnoan tooth plate. Serial, coronal sections through the head of a 57 mm larva of *Protopterus aethiopicus* provide examples of many stages of development from separate to integrated denticles in each ridge of the tooth plate.

The first stage of development in which discrete denticles can be recognized is for convenience termed stage (0) where a cone of pallial dentine is formed at the margins of the dental papilla. In stage (i) of denticle development (Figs 3a, 4) two populations of cells are established within the pulp: those secreting the primary dentine forming the walls of the cone, the odontoblasts; and those forming a distinct tissue inside the cone, the petroblasts, secreting petrodentine. This differs from the dentine in retaining little of the organic matrix and for this reason is presumed to have a higher proportion of
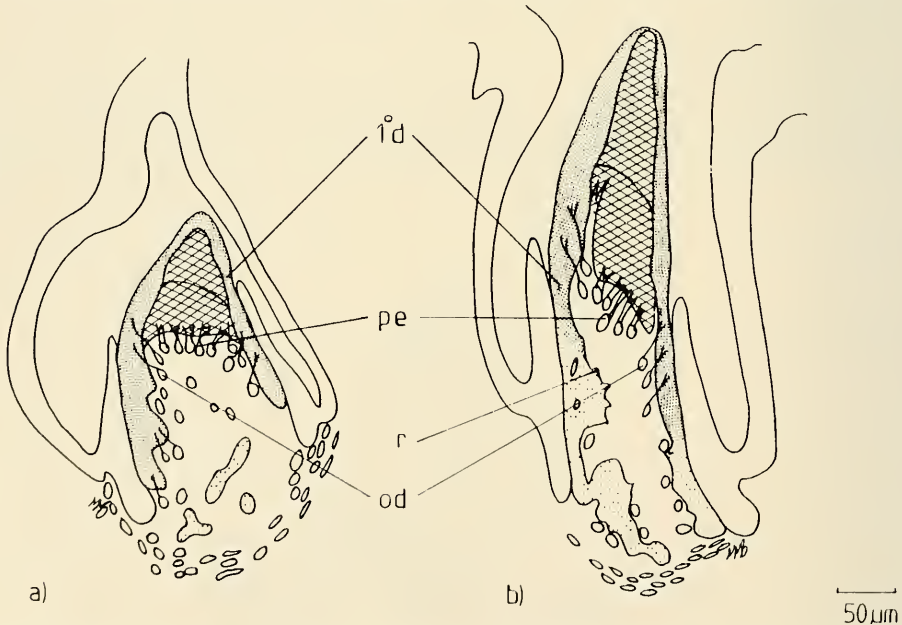
Fig. 3. Protopterus aethiopicus Owen. 57 mm larva; stage (i) and stage (ii) denticles from the prearticular tooth plate, distribution of dentine and petrodentine (Key as in Fig. 1). (a) early formation of petrodentine from petroblasts at the pulp surface. Primary dentine formed earlier in development is extended at the margins from odontoblasts, in advance of petrodentine (b) later stage, ankylosis of dentine to bone of the pedestal, and extension of the height of petrodentine by continued secretion from petroblasts. Space for this growth created by resorption of bone.
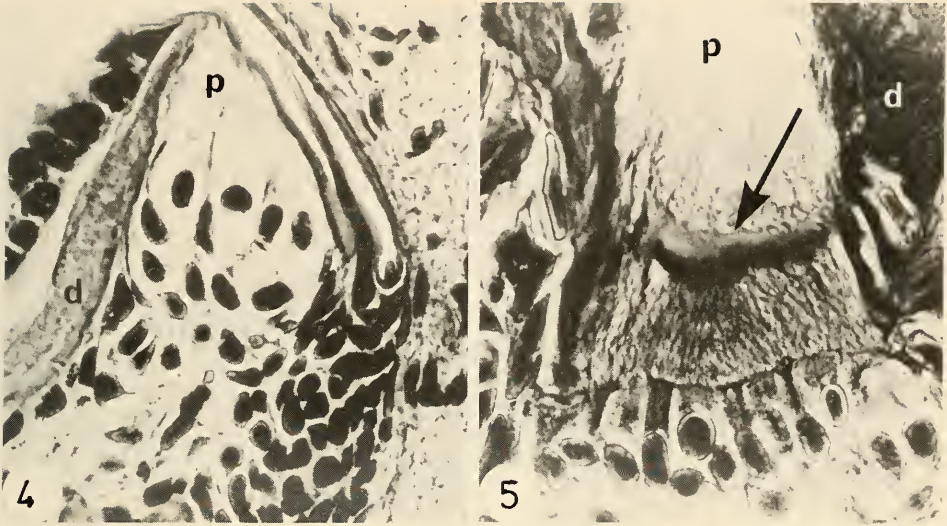
Figs 4, 5. *Protopterus aethiopicus*. 57 mm larva H & E Decalcified, coronal section (P10500). *Fig. 4.* Slightly earlier stage than (3a), pale stained matrix of petrodentine containing cell processes from petroblasts. These are distinct from odontoblasts related to the forming front of dentine. Field width — 150μm. *Fig. 5.* Forming front of petrodentine beneath tritural surface in oldest region of tooth plate. New matrix of petrodentine has a high level of organic matrix in contrast to the mature tissue (p). Petroblasts form an integrated layer at the forming surface, with cytoplasm indicative of secretory activity. Growth line with a concentration of organic matrix separates the new tissue from that formed earlier (arrow). Field width 120μm.

mineral. As growth occurs to increase the height of the denticle the odontoblasts continue to secrete the primary dentine, extending the pallial dentine into that of the pedestal (Smith, 1984), which is in part formed by bone (Fig. 3b). Within this structure petrodentine is added at the formative front by a well organized row of cells (Fig. 5). Beyond the formative front, and parallel to it is a growth line (arrow, Fig. 5) with a greater concentration of organic matrix. This contrasts with the earlier formed petrodentine now devoid of organic matrix, this having been replaced by hydroxyapatite. Resorption of the pedestal tissue occurs in advance of the forming front of petrodentine (r, Fig. 3b), so that new dentine and petrodentine grow into a resorption space in the basal bone of the tooth plate. In this way continuous growth of petrodentine will replace that lost by wear at the tritural surface. The pattern of this replacement growth and its contribution to the changing morphology of the tooth plate is reported elsewhere (Smith, 1984).

2. *PROTOPTERUS AETHIOPICUS* — **Adult**

Vertical sections through one ridge of the tooth plate show the composition of all the tissues that contribute to the whole structure (Fig. 6). These include the bone of the pedestal or bone of attachment, the dentine enclosing the pulp canals, the petrodentine and the superficial layer of enamel (Smith, 1979b). A comparison is easily made in each section between the mature tissue at the tritural surface (Fig. 7) and the new tissue at the forming surface (Figs 8, 9), situated deep within the bone (character 10, Table 1).

i) MATURE TISSUE STRUCTURE — Microradiographs of ground sections show the extremely high degree of mineralization of the petrodentine (character 4, Table 1)
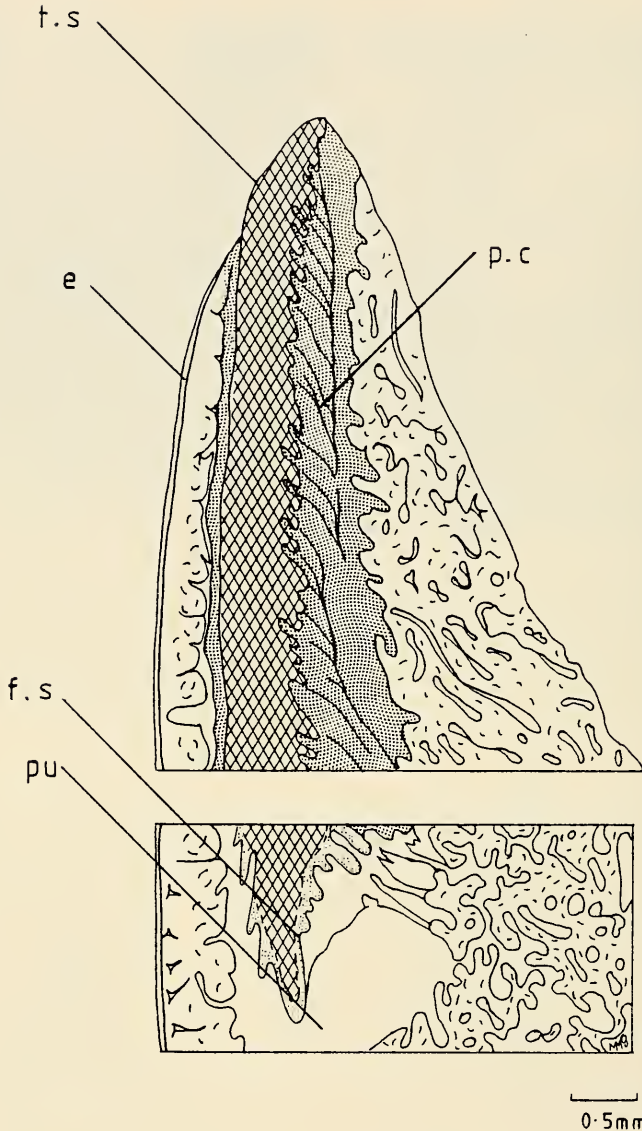
Fig. 6. Protopterus aethiopicus — (G.S., M.R, 47-6, A.449.3) Vertical section through ridge 3 of lower jaw tooth plate. Ridge of petrodentine supported by dentine and bone with a growth surface (f.s) deep to the tritural surface. Pulp canals run from the pulp cavity through the dentine and terminate close to its border with petrodentine. Enamel on the labial margin covers dentine and bone (1/3 of the total height is omitted in the drawing).

relative to the adjacent dentine and bone (Figs 7, 8, 10). This is approximately four and a half times greater in density than the dentine and bone. The only tissue of equivalent opacity to X-rays is the very thin layer of enamel (Figs 7, 8) on the labial and lingual margins of the bone. Decalcified sections (Fig. 9) show that the major part of the petrodentine is removed during processing by the dissolution of calcium salts, leaving only traces of organic matrix at the junctions with the dentine of the pulp canals

and a substantial amount of matrix at the forming surface (character 9, Table 1). None of this organic matrix of the petrodentine is birefringent (character 5, Table 1) in contrast with that of the dentine and bone which shows the birefringence typical of collagen fibre bundles (Fig. 9). The same features are shown in the sections of larval tooth plates (Figs 4, 5). At the tritural surface the major part of the ridge is petrodentine (Fig. 7), supported on either side by bone and linked to this by dentine containing pulp canals (for convenience of description termed trabecular dentine). The pulp canals, each surrounded by dentine (circumpulpal dentine) run into the petrodentine at an angle to the vertical axis of the ridge. In the same position collagen fibre bundles of the trabecular dentine pass into the petrodentine (character 8, Table 1). At this junction the sign of birefringence changes from positive due to the collagen fibres, to negative due to crystals of hydroxyapatite parallel to the fibre bundles. In the petrodentine, the birefringence is due to organized crystal-fibre bundles (shown in s.e.m.'s, Fig. 13) and shows an isotropic zone in the mid-vertical line, with either side of this, positive and negative signs of birefringence in the NW and NE positions relative to crossed polars (character 6, Table 1). Tubules do not extend for any distance into the petrodentine; the bulk of the tissue is atubular (character 3, Table 1).

A block of tissue cut adjacent to the vertical sections (as in Fig. 10) and including also the labial growth margin (Smith, 1984) allows a comparison of the same regions, mature and forming surfaces at a higher level of magnification, using the s.e.m. (Fig. 11). The major part of the tissue between the pulp canals is petrodentine (high mineral density in Fig. 10) and this appears as a basket-weave of crystal-fibre bundles (c.f.b.) (Fig. 12) in which all the crystals lie parallel to each other in one c.f.b. and are at an angle to the adjacent one (Fig. 13). The circumpulpal dentine which contains tubules has a homogeneous appearance (crystals too small to resolve) and has etched to a lower level than the petrodentine. It produces the low density regions in the micro-radiograph.

ii) FORMING TISSUE STRUCTURE — In the microradiograph (Figs 8, 10) the high degree of mineralization of the petrodentine is reached within a very short distance of the formative front (Fig. 8). The forming tissue is low in mineral and high in organic matrix and is secreted by cells (petroblasts) lining both surfaces of the downward growing ridge of petrodentine (Figs 8, 9). Numerous processes from the petroblasts penetrate the forming tissue (Figs 8, 9) and these can be seen as spaces in s.e.m.'s of an anorganic preparation of the forming surface (Figs 14, 15). The organization of the crystal-fibre bundles is established in this region but the individual crystals (presumed smaller) are not as easily resolved as in the mature tissue at the same magnification (Figs 13, 15).

The large pulp canals passing into the petrodentine from the pulp chamber are not, at the initial formative stage, lined with circumpulpal dentine (Fig. 14). The microradiograph (Fig. 10) and the block of tissue in the s.e.m. (Fig. 11) are of equivalent regions (the section being adjacent to the cut face of the block). They show the extent of hypermineralized tissue in this region, and the way in which pulp canals are gradually incorporated into the growing front of petrodentine by a differential cessation in growth of petrodentine at this point. The incorporation of pulp canals later in growth at the formative front is also seen in Figs 8 and 9. In all these regions the new tissue, petrodentine and trabecular dentine, is forming against a resorption surface of the bone, marked by a reversal line or scalloped border (r, Fig. 8). In the same way resorption precedes new growth in the larval tooth plate. More detailed presentation of this information on the relationship between resorption and growth will appear in two papers in preparation.
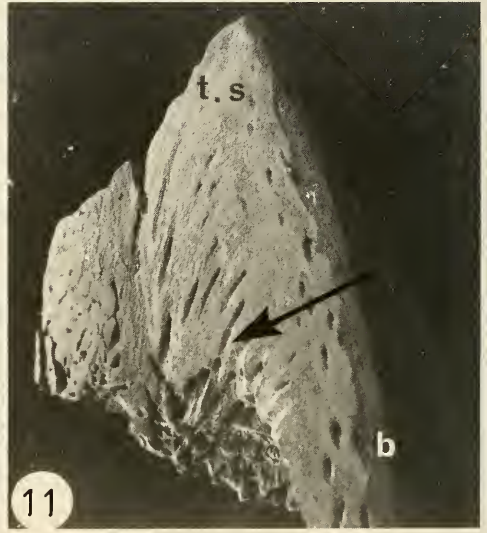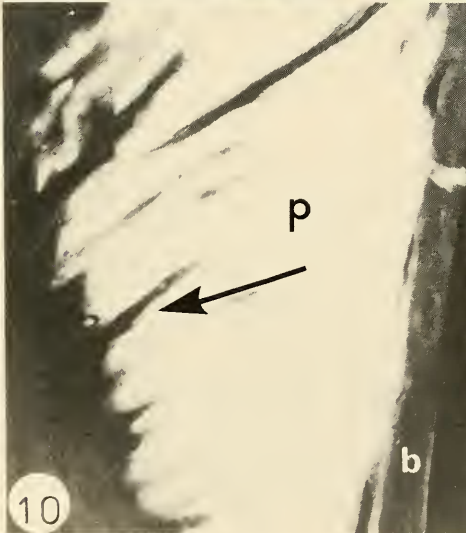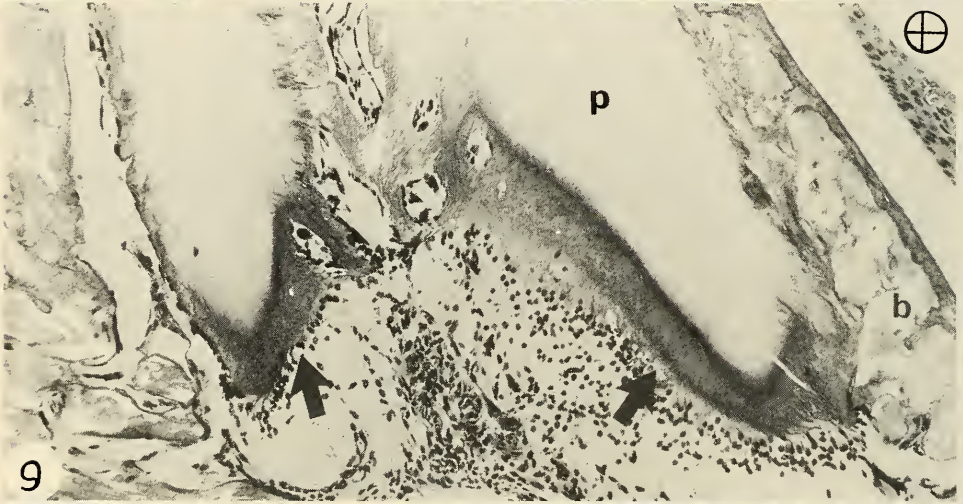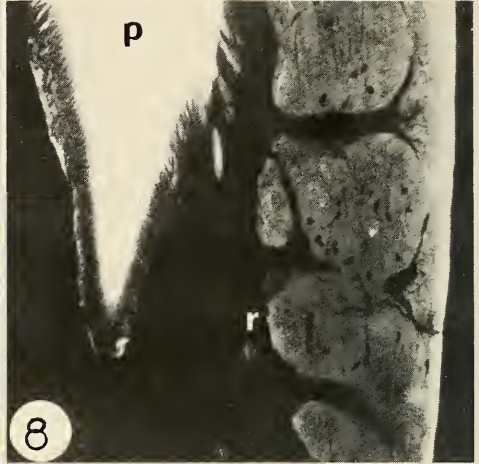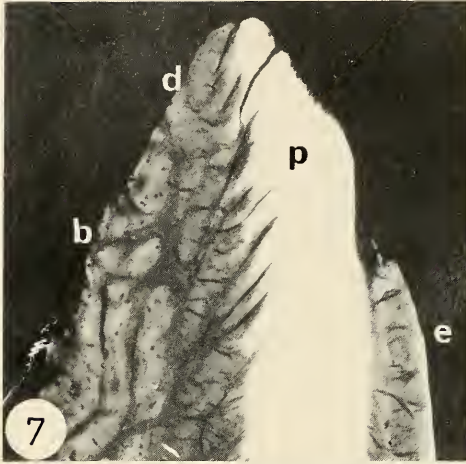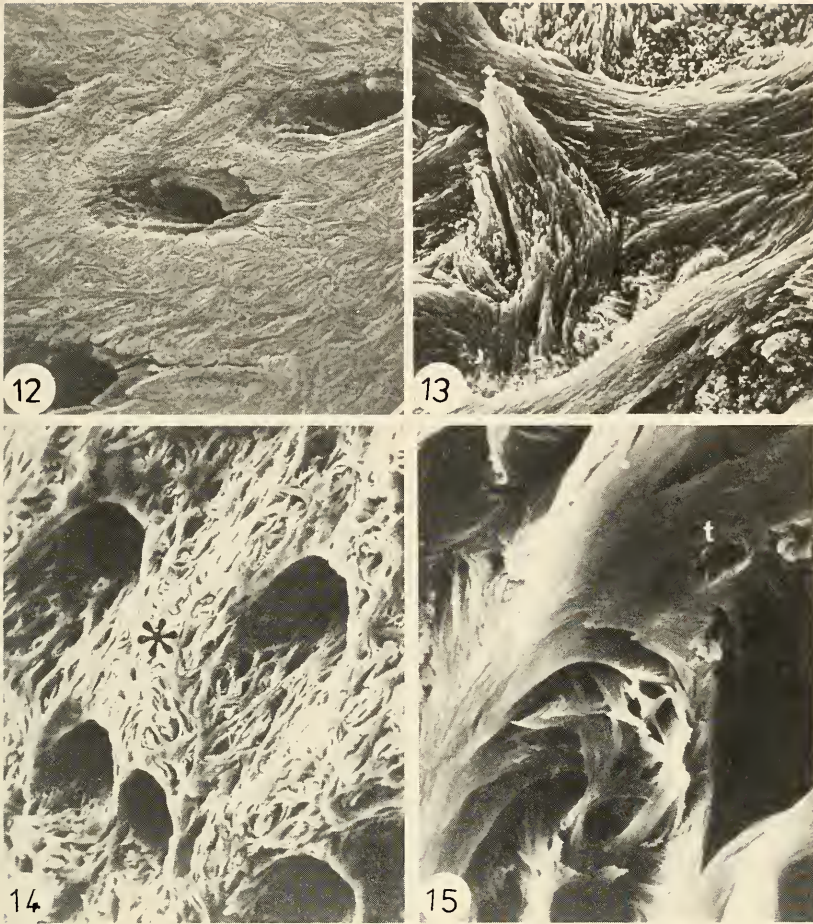
Figs. 7, 8. *Protopterus aethiopicus* (MR 47/6, A449.3) Microradiographs of vertical section through ridge 3 of lower jaw tooth plate. Opacity of petrodentine to X-rays, equivalent to that of enamel (100 μm section, 30kV, 33mA, 10 mins). *Fig. 7.* Tritural surface of abraded petrodentine, dentine and bone. Pulp canals of dentine pass into petrodentine from lingual border. Field width 2 mm. *Fig. 8.* Forming surface (as in Fig. 6, but labial margin on reverse side). Fringe of less mineralized tissue with many tubules at both borders of petrodentine indicates growth from both surfaces. Space for pulp chamber by resorption of bone (r). Field width 0.8 mm. *Fig. 9. Protopterus aethiopicus* (WJ5/49-36) Decalcified section H & E, ½ PL vertical, labio-palatal. Forming surface (arrows) of petrodentine in two adjacent ridges. High content of organic matrix compares with low mineral content in Fig. 8. Petroblasts linked to this surface with short cell processes. Birefringent collagen in the adjacent dentine and bone and the dentine around the pulp canals. Absence of organic matrix in older petrodentine (p). Field width 2 mm. *Figs 10, 11. Protopterus aethiopicus* (45/4a, A.449.3) Microradiograph and adjacent surface as s.e.m block. Labial margin of ridge 2. Lower jaw tooth plate. Many pulp canals from forming surface (arrow) and extensive area of hypermineralized dentine (p) within a shell of bone as in Fig. 9. S.e.m's in Figs 12-15 from this surface. Field widths 1.7 mm and 3 mm. *Figs 12-15. Protopterus aethiopicus* Anorganic specimen s.e.m's of cut, polished, etched surface (0.1NHCl for 1 min) and forming surface lining the pulp cavity. *Fig. 12.* Petrodentine near tritural surface (t.s. Fig. 11), circumpulpal dentine (c.p.d) lining each pulp canal. Field width 310 μm. *Fig. 13.* Parallel crystals in each domain or crystal-fibre bundle from petrodentine in field of Fig. 12. Field width 30 μm. *Fig. 14.* Forming surface from field near arrow (Fig. 11). Many large pulp canals, none with a lining of c.p.d. Numerous small spaces in petrodentine, occupied *in vivo* by organic fibres and cell processes from petroblasts. Field width 310 μm. *Fig. 15.* Field from between pulp canals in Fig. 14 (asterisk). Tubule (t) could be occupied by either cell process or fibre bundle. Same magnification as Fig. 13, but crystallites smaller and not individually resolved. Field width 30 μm.

3. *LEPIDOSIREN PARADOXA*

Microradiographs of vertical labio-lingual sections through the central region of the tooth plate, between ridges two and three, show a much more extensive region of hypermineralized tissue (Fig. 16) than sections through only one ridge of the tooth plate (Fig. 18). The amount of this petrodentine is considerably greater and reaches across the whole width of the tooth plate in this region. It is only interrupted by pulp canals traversing the thickness of the tooth plate from the pulp chamber to the tritural surface (Figs 16, 17 Y). The microradiograph of a vertical section through ridge three (Fig. 18) shows a much narrower region of petrodentine, comparable with that in ridge three of *Protopterus* (Figs 6, 7), and proportionally fewer pulp canals entering from the pulp chamber. All of the pulp canals are walled by dentine that has many branching tubules and a much lower mineral density than the petrodentine. In phase contrast microscopy (Fig. 19) of the same ground section as the microradiograph (Fig. 16) the tubules are seen to radiate from the pulp canal (X in Figs 16, 19), branch, and terminate in fine extensions of the tubules within the petrodentine. Some of these in the petrodentine may be spaces between the crystal-fibre bundles and not necessarily tubules containing cell processes from the odontoblasts. The circumpulpal dentine, tapers to a thin layer at the forming front of the petrodentine and the most recently formed canals are not lined with this form of dentine. S.e.m.'s of the block of tissue adjacent to the section show the typical interlacing crystal-fibre bundles of petrodentine (Figs 20, 21). Some of these crystal-fibre bundles run into the dentine at the junction with the petrodentine (Figs 20, 21). In the s.e.m. of a region of petrodentine near the forming front many fine fibrils, of presumed organic matrix, are associated with the crystal-fibre bundles (Fig. 21). In polarized light microscopy (Fig. 17) of the same ground section as the microradiograph (Fig. 16), the circumpulpal dentine along the length of the pulp canals (X, Y, Z), shows the strong birefringence due to collagen fibres. An isotropic line occurs at the junction between circumpulpal dentine and petrodentine (Fig. 17) where the birefringence due to the mineral cancels out that due to the collagen fibres. In the narrow regions of petrodentine, birefringent bands (due to crystal-fibre bundles) of opposite sign of birefringence, run at 45° to the vertical axis. Also in the larger masses of petrodentine the birefringence appears as a basket-weave of opposite signs of birefringence (asterisk, Fig. 17).

4. LEPIDOSIRENIDS — Fossil forms

Two examples of tooth plates from fossil species of *Protopterus* and *Lepidosiren* have been sectioned — *Lepidosiren* sp. (Fig. 22) from the Upper Miocene in Colombia, from the same locality as the specimens figured as whole tooth plates and s.e.m.'s by Ørvig (1976b: figs 20-25), and *Protopterus* sp. from the Eocene in Mali. The distribution of the tissues petrodentine, trabecular dentine and bone as they appear within the sections (Figs 22, 23) depends to a great extent on both the individual age of the tooth plate, and the position in the tooth plate through which each section was cut. The tissue contributing to the wear-resistant parts of the ridges on the tritural surface is petrodentine: the histology and ultrastructure is similar to that described in the extant forms. In both *Lepidosiren* sp. and *Protopterus* sp. distinct growth lines can be recognized, parallel to the forming surface and spaced out at regular intervals, at a steep angle to the tritural surface (Figs 22, 23). Pulp canals run from the pulp chamber towards the margins of the petrodentine branching initially within the trabecular dentine; finer branches continue into the petrodentine. The section of *Lepidosiren* sp. (Fig. 22) is vertical through the tooth plate and is the first one adjacent to the medial symphysis. It illustrates an unusual feature of growth in these genera, viz. that growth can occur from both labial and medial or palatal aspects (Smith, 1984). The section of *Protopterus*
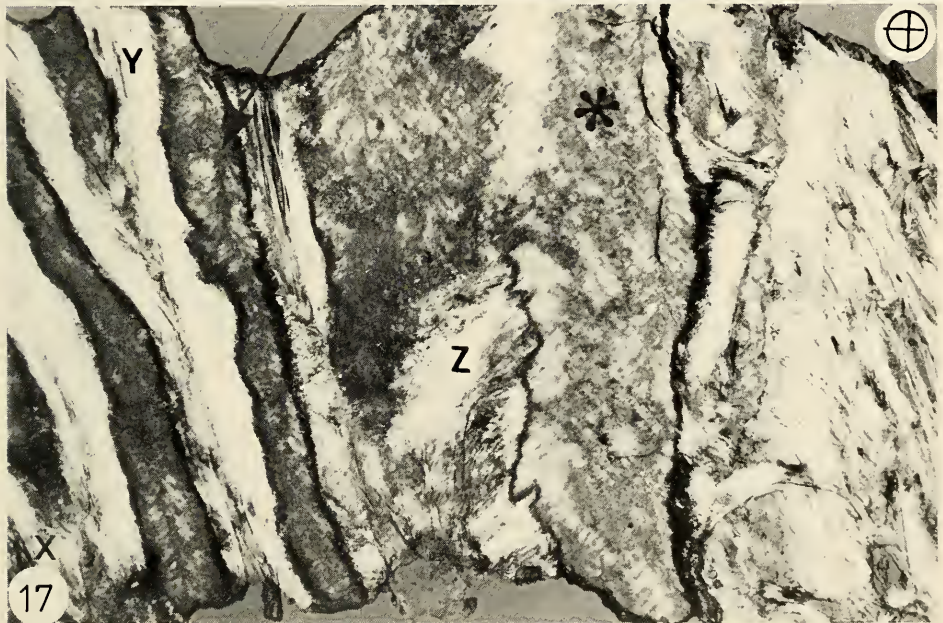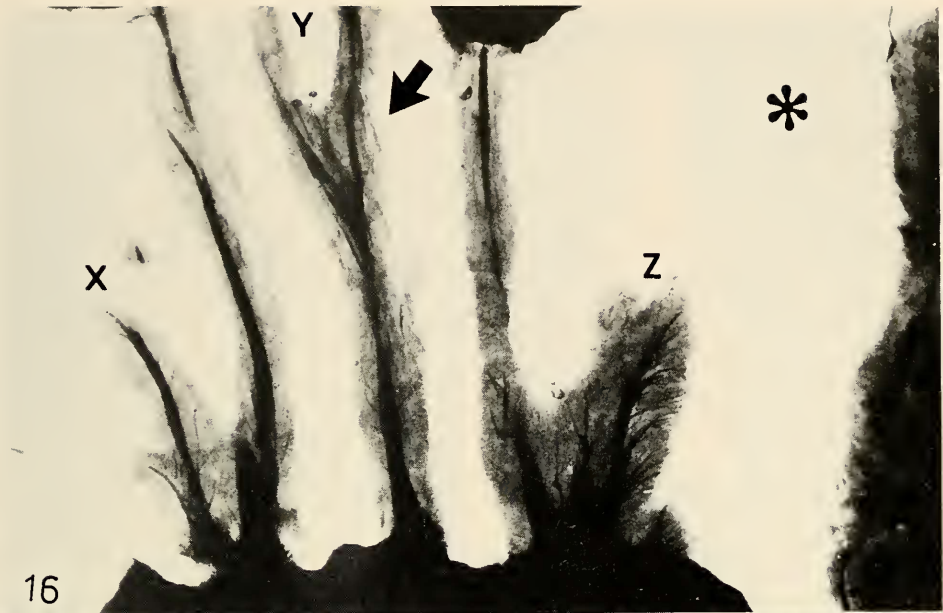
Figs 16, 17. *Lepidosiren paradoxa* Natterer (65/4) Labio-lingual, vertical ground section through central area joining R_2 and R_3, corresponding pulp canals (X, Y, Z) pass from the forming surface to the tritural surface. Typical area of petrodentine (asterisk, Fig. 16) shown as alternate bands in polarized light (Fig. 17) and as opaque to X-rays in microradiographs (Fig. 16). c.p.d. strongly birefringent, with tubules and less dense to X-rays. Field width 1.5 mm.
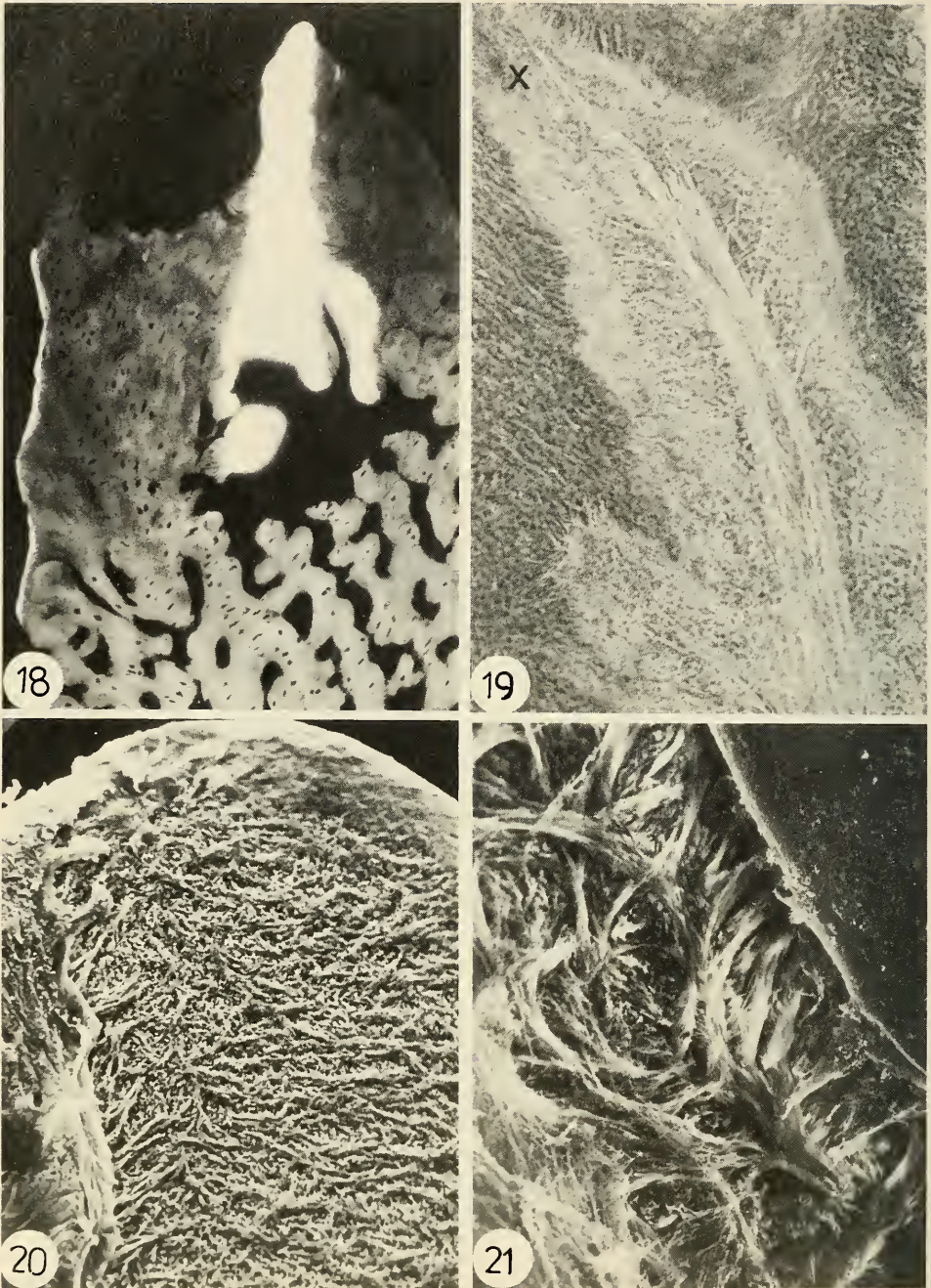
Figs 18-21. Lepidosiren paradoxa.
Fig. 18. Microradiograph of adjacent sections to Figs 16 & 17, shows petrodentine of R_3, and enamel layer. Tissues compare with Figs 7 & 8. Field width — 2 mm. *Fig. 19.* Phase contrast of pulp canal X in Figs 16 & 17, tubules from pulp canal pass through c.p.d. and stop at junction with petrodentine. Field width — 280 μm. *Fig. 20.* S.e.m. of adjacent cut, polished, etched surface, shows petrodentine near tritural surface, of the same ridge as in Fig. 18. Field width — 310 μm. *Fig. 21.* S.e.m. of same ridge only near forming surface. Shows crystal-fibre bundles of petrodentine merging into dentine. Field width — 62 μm.
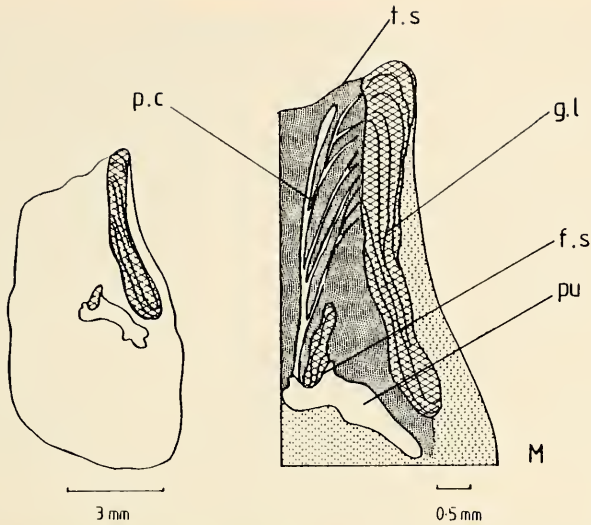
LEPIDOSIREN SP. MIOCENE: COLUMBIA PF 9005

UPPER TOOTH PLATE - R^4, S^1

Fig. 22. Lepidosiren sp. Vertical section through the entire upper tooth plate and bone parallel to the medial symphysis, shows amount of petrodentine relative to bone and dentine. Detail of growth lines and pulp canals.

sp. (Fig. 23) shows the main region of growth of ridge one at the labial margin. Here there is an extensive forming surface of petrodentine and a free margin not attached to the bone. This is directly comparable with the part of the tooth plate of *Protopterus aethiopicus* shown in Figs 10 and 11. In both these sections (Figs 22, 23) patches of petrodentine are found separated from the main region by trabecular dentine and bone. They relate to the side-ribs of the other ridges (ridge 2,3) and to new, smaller regions of growth on the medio-palatal aspect.

5. *NEOCERATODUS FORSTERI*

Vertical sections along one ridge of the tooth plate (Figs 24, 25, 26) together with horizontal sections across two ridges (Figs 27, 28, 29) show the distribution of the tissues, the arrangement of the pulp canals and the composition of the two types of dentine. These can be compared with Ørvig (1976b: figs 13, 14, 19), of which two figures were redrawn from Günther (1871). The hypermineralized dentine, labelled as pleromin by Ørvig (1976b), is all of the tissue between the parallel, evenly-spaced pulp canals passing from the formative surface to the tritural surface. In microradiographs the appearance is similar to that shown in *Lepidosiren* (Fig. 16). In a horizontal section showing the bifurcation between two ridges (Fig. 29) the petrodentine is the entire amount of tissue between the pulp canals and adjoins the bone at the labial and medial margins. The bone is most extensive at the mid-point between two ridges (Fig. 29) and is confined to a very thin border at the labial extremities of each ridge. Kemp (1979: figs 13A, E) has illustrated a similar distribution of tissues in a horizontal section through the adult tooth plate. In the decalcified sections most of the matrix of petrodentine has been removed leaving only thin strands staining with alcian blue (Figs
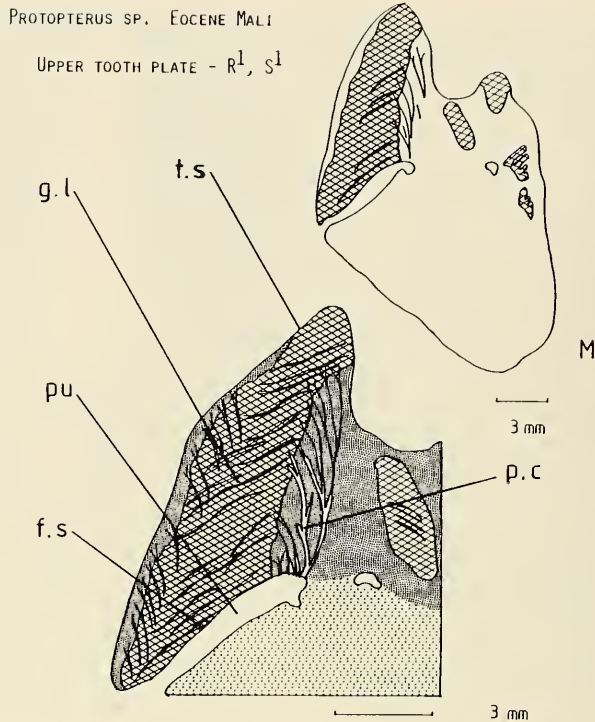
Fig. 23. *Protopterus* sp. Vertical section through bone and petrodentine, labio-palatal plane, of first ridge (R¹) in upper tooth plate; patches of petrodentine in medial part. Detail of growth lines and pulp canals.

24, 26). In the horizontal ground sections (Figs 27, 28) the petrodentine is translucent, lacks tubules, and in polarized light shows a high degree of preferred orientation of the crystal-fibre bundles in a radial arrangement relative to the pulp canals (Fig. 28). This observation is in agreement with Ørvig (1976b: fig. 19). In the equivalent s.e.m.'s of the block adjacent to the ground sections (Fig. 30) the petrodentine etches less deeply than the circumpulpal dentine and is composed of the typical large crystals (Fig. 34) arranged as crystal-fibre bundles, some arranged radially and some at an angle to these, lying in the vertical plane of the section (Figs 30-33).

The pulp canals are lined with dentine some of which completely infills the canal towards the tritural surface (Fig. 24). This circumpulpal dentine is less opaque to X-rays (Fig. 29), and retains a high proportion of organic matrix in decalcified sections (Figs 24, 26); this remaining organic matrix is strongly birefringent in contrast to the matrix of the petrodentine (Fig. 25). In horizontal ground sections the birefringence of the circumpulpal dentine is delineated by an isotropic line at the junction between the

Figs 24-26. *Neoceratodus forsteri* Krefft (BM(NH) — 5005) Decalcified, Alcian Blue and Safranin (fig 3, pl 2, LP Plan, White, 1966). Vertical section through upper tooth plate in central region of tritural surface. Figs 24, 25. Thin strands of organic matrix remain in the petrodentine. In contrast, much organic matrix remains around pulp canals, strongly birefringent in polarized light (arrows). Field widths — 3 mm. *Fig. 26.* Phase contrast of two pulp canals near tritural surface, tubules for odontoblast cell processes in c.p.d. and infilling dentine (asterisk) in pulp canals. Some organic fibres link into petrodentine/dentine (c.p.d.) junction. Field width — 0.5 mm.
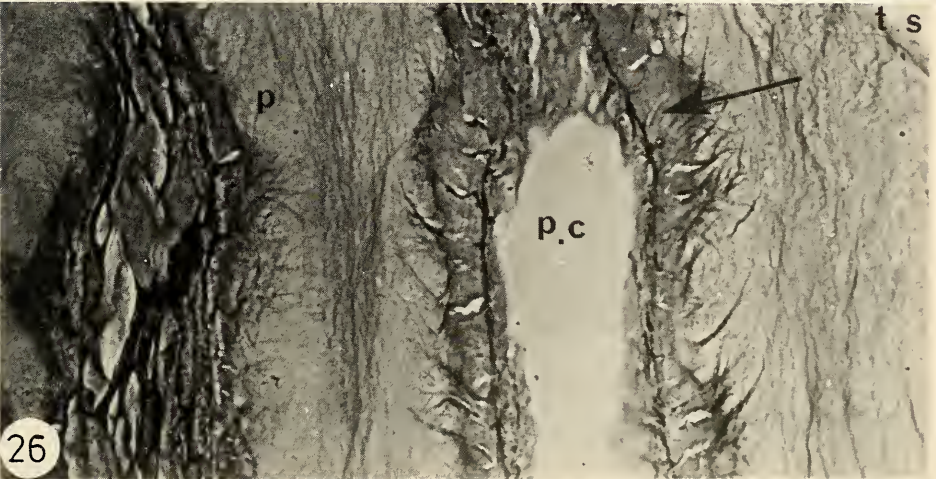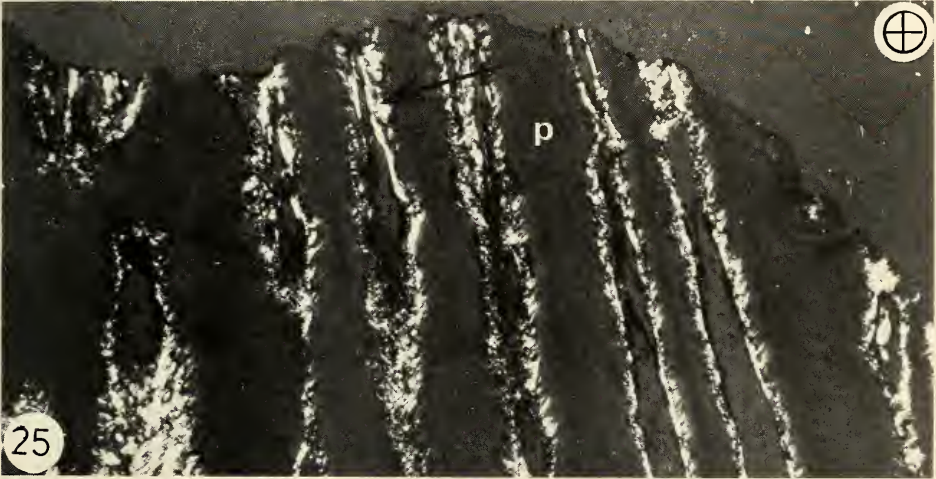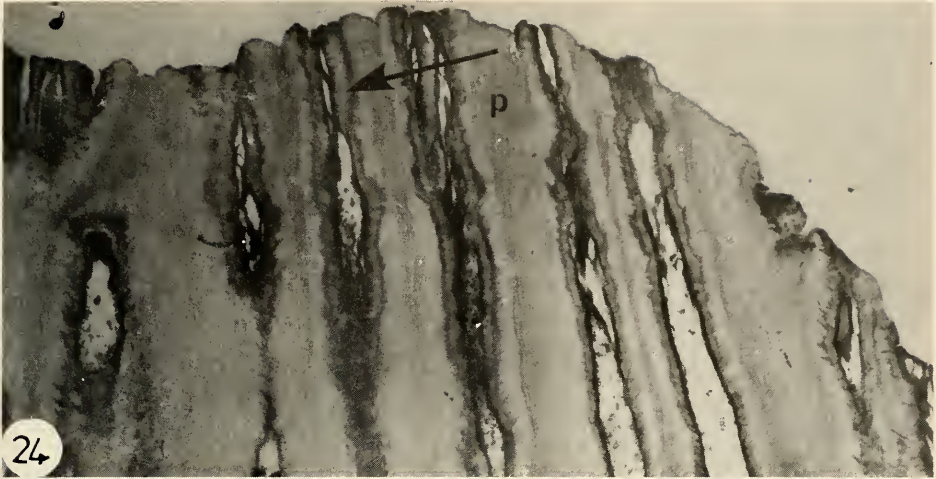
tissues (Fig. 28) where the sign of birefringence changes. This dentine shows a dark polarization cross in the position of the polarizer and analyser, reflecting the radial or concentric arrangement of the collagen fibres. Spaces housing cell processes from the odontoblasts run through the circumpulpal dentine, ending as fine processes in the adjoining petrodentine (Fig. 26). Other fine fibrils lie parallel to these tubules and run into the petrodentine as continuations of the collagen fibre bundles. Both these structures provide links across the junction between circumpulpal dentine and petrodentine. Comparing a younger region of the tooth plate with an older one (Figs 31, 32), the difference in the surface of the pulp canals is apparent; in the mature tissue only is there a lining of circumpulpal dentine and this is shown both by the microradiographs and by the longitudinal sections. In the younger tissue the surface to the pulp canal is petrodentine (Figs 31, 33), and several tubules assumed to contain cell processes are present (Fig. 33). The large-sized crystals are arranged in groups, lying parallel to each other and at an angle to the next adjacent group (Fig. 34).

    In this way the pattern of development of the tissues in the tooth plate is shown to be characterized by (1) the formation of petrodentine from the surface lining the pulp chamber, leaving spaces for vascular pulp canals, and (2) by the narrowing of each canal by the secretion of a lining of circumpulpal dentine over the original surface of the petrodentine. At a lower level in the tooth plate the surface of petrodentine continues to grow deeper into the bone as space is created by resorption of bone (Smith, 1984). This process of histogenesis is the same as in *Protopterus* and *Lepidosiren*.

6.   CERATODONTIDS — Fossil forms

    The tooth plates of several species of *Ceratodus* have been investigated and the structure compared with those of *Neoceratodus*. Material has been examined optically in thin sections and by s.e.m. whenever both have been possible.

i) *Ceratodus madagascariensis* Priem. Sections, figured as low-power plans of the tooth plate by White (1966: fig. 2, pl. 2), are of a tooth plate from the Upper Cretaceous. The pulp canals are as regularly arranged as in *Neoceratodus* (White, 1966: pl. 2, figs 2, 3) and the tissue between the pulp canals shows a very regular arrangement of crystal-fibre bundles when viewed in polarized light (Figs 35, 36). There is a neutral zone at the mid-point between adjacent canals and either side of this the crystal-fibre bundles show opposite signs of birefringence, features typical of the high degree of organization of crystals in petrodentine. Sections viewed in phase contrast allow the tubules to be clearly identified (Figs 37, 38), and these are shown running into the petrodentine from the pulp canals; it is assumed from their shape and size that they contained cell processes from the body of the odontoblast cell in the pulp canals. Comparison of a forming surface (Fig. 37), with a more mature region situated towards the tritural surface (Fig. 38) shows that in the forming region the pulp canal is not lined with circumpulpal dentine. The pulp canals in the older zones of the tooth plate have a lining of circumpulpal dentine; this tissue is not birefringent, has become stained during fossilization, and the tubules run through it into the petrodentine from the surface of the pulp canal. The arrangement and proportion of these tissues in the tooth

Figs 27-29. *Neoceratodus forsteri* (41/1-3). Horizontal ground section across two ridges of upper tooth plate. Field of region of indentation between ridges at labial margin.
Figs 27, 28. Same area in ordinary and polarized light. Very thin layer of bone merges into thicker bone (top right) at junction between ridges. Isotropic lines mark junctions between c.p.d. and petrodentine, where the sign of birefringence changes as mineral exceeds collagen fibres. Field widths — 2.5 mm. *Fig 29.* Microradiograph of adjacent section, bone at deepest point of indentation between ridges. Petrodentine totally opaque to X-rays, some canals lined by less dense circumpulpal dentine. Field width — 4.2 mm.
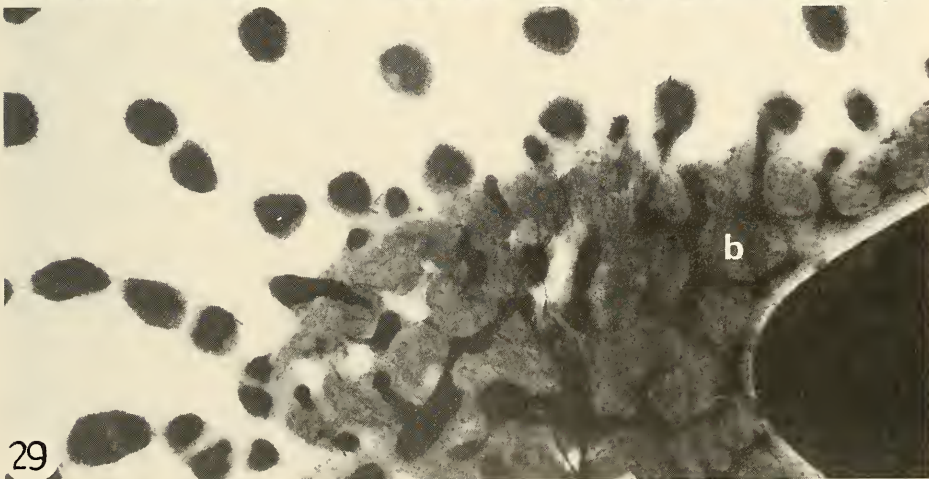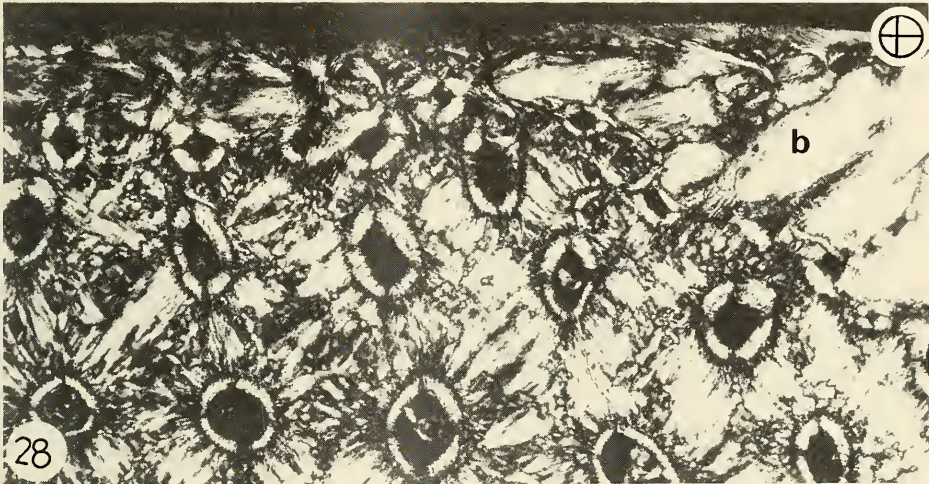
plate of *Ceratodus madagascariensis* is compared with that of *Neoceratodus, Lepidosiren* and *Protopterus* in the final diagram (Fig. 57).

ii) *Ceratodus runcinatus* and *Ceratodus kaupi*. Tooth plates of specimens from the Triassic of West Germany have been sectioned and s.e.m.'s made from the adjacent block surfaces. The arrangement of the pulp canals throughout the tooth plate is very regular as in most ceratodontids and they run from the forming surface to the tritural surface (Smith *et al.,* 1984: fig. 1). Growth lines are very conspicuous and form a series in the petrodentine parallel to the forming surface. This, and other aspects of growth are discussed in Smith *et al.* (1984). The arrangement of pulp canals in these tooth plates was compared with those of *Neoceratodus.* Both horizontal and longitudinal sections of *Ceratodus runcinatus* have been illustrated by Günther (1871: figs 4-6, pl. 33). In polarized light the properties of the tissue between the pulp canals are identical with those described for *Ceratodus madagascariensis* — that is, strong birefringent bands at 45° to the pulp canals with opposite signs of birefringence. There is a difference between *Ceratodus runcinatus* and *Ceratodus kaupi* in that the latter shows more interwoven crystal-fibre bundles.

In s.e.m.'s the tissue between the pulp canals etches less deeply and has larger crystals than the circumpulpal dentine, and is arranged as a felt-work of crystal-fibre bundles (Figs 39, 40, 43, 44). Ørvig (1976b: figs 15, 16, 17) has also illustrated these features in Triassic ceratodontids, in which he refers to denteons around the vascular canals and pleromin as the interstitial tissue. Etching of the surface by a different acid reveals the organization of the crystals within the crystal-fibre bundles (Fig. 41), each one with many parallel crystals and variation in the orientation of adjacent bundles. These are all features of petrodentine. Confirmation of the differences in mineral density is given by the back-scattered electron image of the same tissue surface (Fig. 42). The density of petrodentine, being much greater than circumpulpal dentine, results in the lighter appearance of the petrodentine. The darker regions are those around the pulp canals and these are due to less dense packing of the mineral phase. This circumpulpal dentine is added in concentric layers to the surface of the petrodentine as a lining to the pulp canal (Smith *et al.,* 1984: figs 11, 12).

The fine details of organization of the crystals into crystal-fibre bundles appear to be slightly different in the two species, but the specimens of *C. kaupi* examined with the s.e.m. are of tooth plates from a young individual. However, the polarized light appearance is also different in many sections and it could reflect a real difference between the species in the organization of the matrix and crystals. Further observations using s.e.m. preparations are needed.

7. *SAGENODUS INAEQUALIS* Owen

The growth of tissues in the tooth plates of this genus from the Carboniferous has been previously discussed (Smith, 1979a) and the conclusion reached that petrodentine is present in the tooth plates of *Sagenodus inaequalis*. It is, however, worth including

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Figs 30-34. *Neoceratodus forsteri* S.e.m.'s of block of tissue adjacent to sections in Figs 27-29 (etched 1 min. 0.1 NHCl). *Fig. 30.* Crystal-fibre bundles of petrodentine in radial arrangement between pulp canals. Lining of dentine (c.p.d. — deeper etch depth) around older pulp canals. Field width — 625 μm. *Figs 31, 32.* Comparison between pulp canal near to forming surface, without a lining of c.p.d. and canal in older region in which petrodentine is lined with dentine (c.p.d.) with tubules, around the pulp canal. Field width 130 μm. *Fig. 33.* Higher magnification of Fig. 31 shows tubule in petrodentine (arrow) and crystals of c.f.b.'s lining the wall of the pulp canal. Field width — 32.5 μm. *Fig. 34.* Domains of crystals, parallel in each c.f.b. but opposite directions in adjacent bundles. Field width — 13 μm.
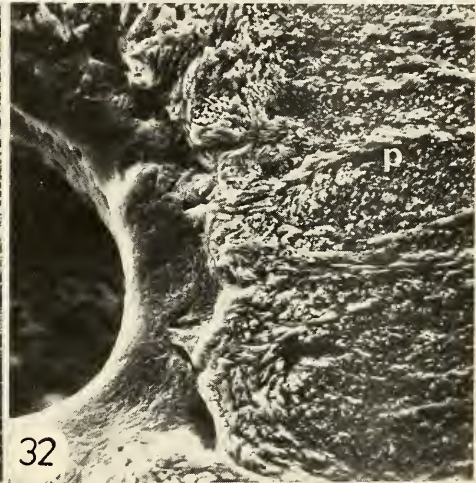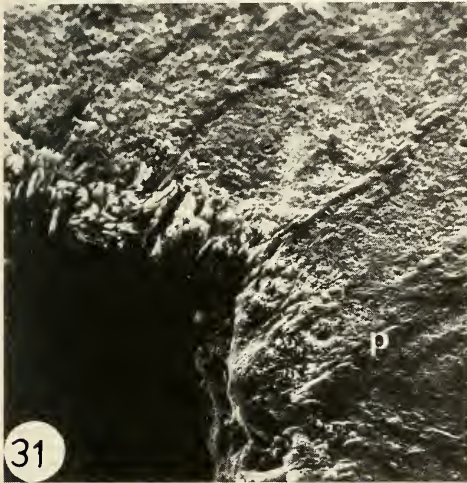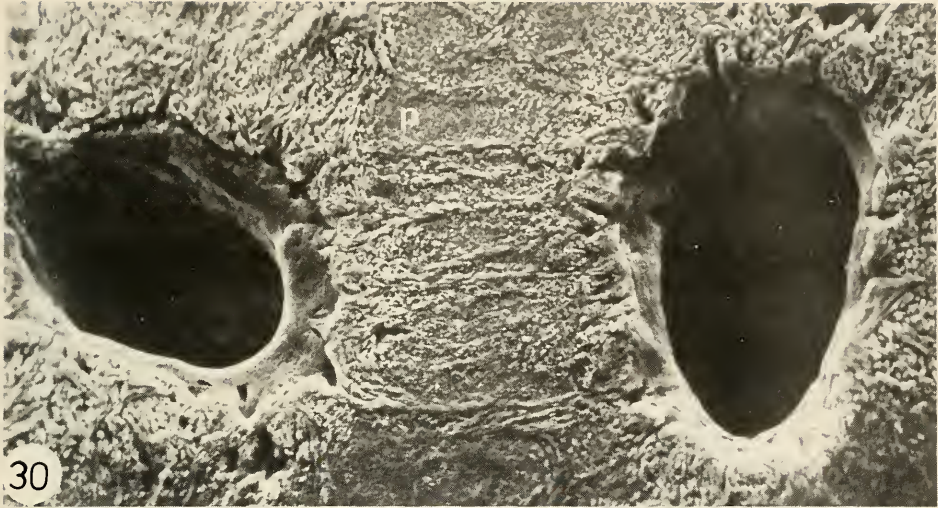
some additional information. The arrangement of the pulp canals in each denticle of the ridges is very irregular relative to those in the ceratodontids (Fig. 45). Only the central part of each denticle along each ridge has tissue with some of the properties of petrodentine (Fig. 47) and this region grows at a forming surface bordering a small pulp chamber. The tissue between the pulp canals is translucent, and was unstained during fossilization, but is relatively weakly birefringent, showing the same sign of birefringence over larger areas than is typical for petrodentine. The organization of this tissue is clearly different from the circumpulpal dentine lining each pulp canal (Fig. 48), but only s.e.m.'s will show how the crystals are arranged. Tubules run through the circumpulpal dentine passing into the petrodentine for a short distance. At the ends of the pulp canals the main tubules branch freely and terminate in many fine extensions within the petrodentine (Fig. 46). As in the lepidosirenids, large areas of bone and trabecular dentine separate the regions of petrodentine both along each ridge, and between the ridges (Fig. 47, and Smith, 1979a: fig. 9).

8. *DIPTERUS VALENCIENNESI*

Two sections have been examined. One is in a vertical plane through one denticle of the tooth plate (Figs 49, 50). The same section is figured as a low-power plan by White (1966: pl. 1, fig. 2). The second is in a horizontal plane through the base of one denticle of the tooth plate (Fig. 51). The pulp canals have an irregular arrangement and run from a small pulp chamber into the denticle where they branch towards the tritural surface (Figs 49, 50). This is the type of arrangement shown in the diagram from Gross (1956) in Fig. 1. In some regions the pulp canals merge with the medullary spaces of the spongy bone; in others a slightly enlarged space occurs beneath the dentine. For convenience this is called a pulp chamber (pu, Fig. 50). The tissue constituting the central part of each denticle is different from that at the margins and at the base. It has many of the properties of petrodentine, being trans-lucent, unstained, and without tubules (Fig. 49). Bands of birefringence of opposite signs produce a woven appearance in polarized light (Fig. 50). In the horizontal section at the base of a denticle, birefringent bands, also of opposite signs and assumed to be crystal-fibre bundles, lie between the tissue surrounding the pulp canals. These are crystals with a preferred orientation in the horizontal plane. In the tissue surrounding the pulp canal the preferred orientation of the crystals is in the vertical plane, parallel to the pulp canals. Only a very thin region of circumpulpal dentine is observed surrounding the pulp canals towards the tritural surface. This has tubules and growth lines concentric with the canal. Growth lines are not observed within the petrodentine, although growth appears to result in the addition of petrodentine to the basal surface. It is also apparent that invasive growth of petrodentine occurs within the adjacent spongy bone (pleromic dentine, Smith, 1977).

The s.e.m. appearance of this tissue in *Dipterus* sp. is typical of petrodentine in that crystal-fibre bundles are arranged in a basket-weave throughout the tissue (Ørvig, pers. com.) with two distinct zones of preferred orientation as described from the observations in polarized light.

9. *CHIRODIPTERUS AUSTRALIS*

The tooth plates of *Chirodipterus australis* Miles from the Late Devonian have been studied and figured previously (Smith, 1977: figs 16, 70-75). The structure of the dentine and arrangement of the tissues in sections through the tooth plate and s.e.m.'s of the tritural surface of a worn part of the tooth plate were described. It was shown that growth lines separate regular segments of the tooth plate and that these are parallel to the forming surface, lining one surface of an extensive pulp chamber (Smith, 1977: fig.
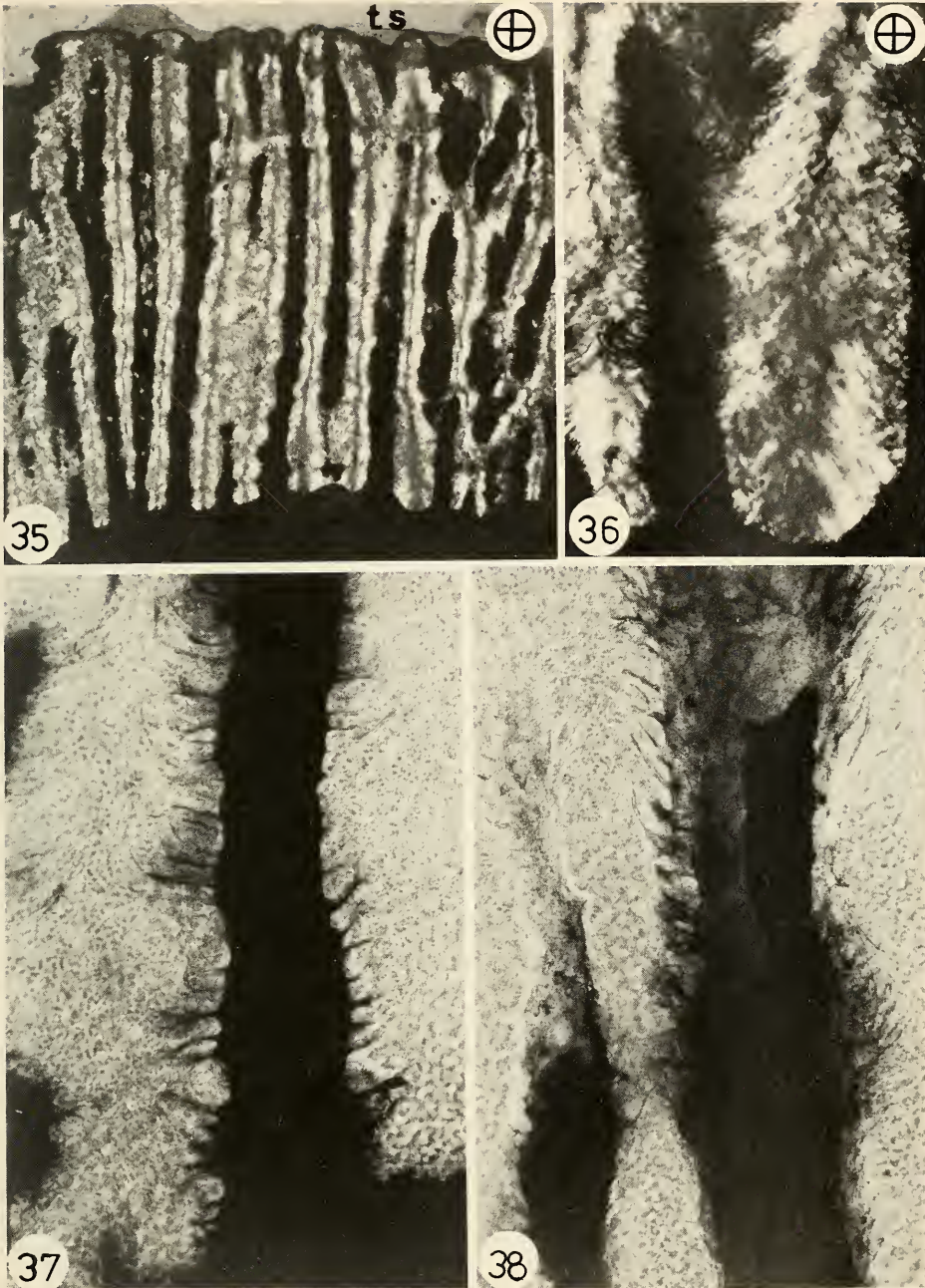
Figs 35-38. *Ceratodus madagascariensis* Priem P15660, BM(NH) (fig. 2, pl. 2, White, 1966) Upper Cretaceous. Vertical section, upper tooth plate.
Fig. 35. Regular arrangement of parallel pulp canals from pulp chamber to tritural surface. Field width — 5 mm. *Fig. 36.* Birefringent tissue between pulp canals has arrangement typical of petrodentine, bands at 45° to pulp canals. Field width — 0.6 mm. *Fig. 37.* Forming surface, tubules pass into petrodentine from pulp canal. Field width — 0.3 mm. *Fig. 38.* Older parts of canal are lined with c.p.d. and tubules pass through this into petrodentine. Field width 0.3 mm.

16). Pulp canals run into the dentine from the pulp chamber and branch irregularly throughout the dentine (Smith, 1977: fig. 70). Although it was reported that the major part of the dentine between the pulp canals is probably equivalent to petrodentine in other dipnoan tooth plates, the relatively limited observations made such a statement inconclusive. Further sections of specimens prepared while the tooth plate was still in the limestone matrix have made possible s.e.m. observations of dentine at all levels from the forming surfaces through to the mature tissue. These have allowed more accurate interpretation of the tissue components of the tooth plate.

The tritural surface is relatively unworn at the labial margin of the tooth plate where it carries a number of rounded tuberosities on the surface. In a section of this region (Fig. 52) the pulp canals are wide at the pulp surface, then branch, anastomose and taper to become very thin at the tritural surface. The tissue between the canals is strongly birefringent and in some regions this birefringence is assumed to be due to parallel orientation of crystals as crystal-fibre bundles. These are arranged in alternate directions, with each c.f.b. showing an opposite sign of birefringence. This is particularly apparent in the younger tissue at the labial margins. In other regions there is principally one preferred orientation of the crystal-fibre bundles.

In an s.e.m. of the surface adjacent to the sections, both forming tissue and mature tissue are observed (Fig. 53). The growth lines are accentuated by etching and appear similar to those described in *Ceratodus runcinatus* (Smith *et al.,* 1984). The lower border of the petrodentine has also etched more deeply (Fig. 53) than the rest and this is interpreted as a less highly mineralized growth zone where a new layer of petrodentine is forming from cells lining the pulp cavity. The pulp canals are wide invaginations along this margin, each bordered only by petrodentine. In the regions near the tritural surface a thin lining of circumpulpal dentine has formed around the canals. The petrodentine between the canals has an intricately woven arrangement of crystal-fibre bundles with many small tubular spaces between them (Fig. 55). The same appearance is seen on the etched tritural surface (Fig. 54) where the circumpulpal dentine is etched more deeply. At higher magnifications the individual crystals can be resolved (Fig. 56) and although in some regions they are all parallel in bundles, in others they appear to be relatively disorganized. It may be found that the detailed crystal arrangement varies between the dental tissues of different dipnoans. This could be attributed to the different responses of the cells forming each tissue to the functional requirements of the tooth plates.

CONCLUSIONS

From the critical review of the literature and from new observations on both extant and fossil dipnoan tooth plates, a clear definition of petrodentine has emerged and a set of criteria proposed — Table 1. Because petrodentine is a term first used for dipnoan tissues (Lison, 1941), and because it is not ambiguous, it is preferred to the term pleromin. Both vascular and compact types of pleromin have been described (Ørvig, 1967, 1976a,b). It is possible also to describe the arrangement of petrodentine as vascular or compact. The combination of methods used in this investigation is

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essential to decide whether the dentine of a tooth plate is in part composed of this special type of extra-hard tissue. Quantitation of the degree of mineralization would, obviously, add to the descriptive data presented in this paper. At present only ap-proximate values can be given for radiological density from the microradiographs of extant forms, petrodentine being 4.5 times as dense as dentine and bone. The nominated criteria can be successfully applied to both extant and fossil forms.

Petrodentine as defined here is not confined to advanced dipnoans, but is present in forms such as *Dipterus* and *Chirodipterus* which extend back to the Middle Devonian. Both Denison (1974) and Ørvig (1976) suggested that a type of hypermineralized dentine is present in some Devonian forms. In *Dipterus valenciennesi* petrodentine is confined to the denticles of each ridge but in *Chirodipterus australis* it forms a larger part of the tooth plate, being extensive beneath the tritural surface. It has not been possible to enlarge upon the comments made previously on the tooth tusks of *Holodipterus gogoensis* Miles (Smith, 1977), where the tissue type is not certain.

From the observations presented here and those in previous publications it is concluded that petrodentine is present in all the extant forms. The only real differences between forms are the arrangements of the vascular pulp canals within the petrodentine and the angle that the formative front of petrodentine presents to the tritural surface. Most of the general features of histogenesis and growth are shared by the extant and fossil forms. That is, growth of petrodentine occurs at the surface deep to the tritural surface within a space created by resorption of bone. This growth surface may be extensive or very narrow but in either case growth of petrodentine is dif-ferential. Where a vascular pulp canal becomes included in the surface as an in-vagination, growth of petrodentine in that region has ceased. This canal then becomes narrower by a lining of circumpulpal dentine laid down by odontoblasts, each one leaving fine branches in the petrodentine and tubules connecting these with the pulp canal. Lison (1941) suggested two possible methods by which the canals at the centre of the trabecular dentine might have originated; the first by resorption, and the second by localized absence of growth of the roof of the pulp chamber. The latter is supported by the present investigation. Denison (1974) thought that the pulp canals had migrated from a position beneath the centre of the denticles to a position at the sides. This was suggested to him by the arrangement of tissues in *Monongahela,* and by the position of the pulp canals in *Protopterus* at the margins of the ridges.

The arrangement and growth of petrodentine in Tertiary lepidosirenids is similar to that in the extant forms, and its arrangement and growth in fossil ceratodontids as old as the Triassic is similar to that in the extant *Neoceratodus*. Genera differ in the microstructure of their tissues, that is in the arrangement of the vascular canals, and in the proportions of petrodentine to trabecular dentine. These differences include the pattern of the crystal-fibre bundles which may be dependent on function, as well as the branching and extent of penetration into the petrodentine of the tubules from the cells in the pulp canals.


Figs 42-44.
Fig. 42. Ceratodus runcinatus Spec. No. PV19279 IMGP — Tübingen. Polished, non-etched surface, back-scattered electron image. No topography on surface (except scratches from polishing and holes where pulp canals are empty). Contrast shows differences in mineral density, petrodentine being more densely mineralized than dentine around pulp canals. Field width — 177 μm.
Figs 43, 44. Ceratodus kaupi Agassiz PV4460 IMGP — Tübingen. Triassic. *Fig. 43.* Vertical, cut surface through small tooth plate. Forming surface of petrodentine (arrow) pulp canals with very thin lining of c.p.d. Most of tooth plate is formed from interwoven crystal-fibre bundles. Field width — 730 μm. *Fig. 44.* High power of central area of petrodentine shows many alternating crystal-fibre bundles. Field width — 45 μm.
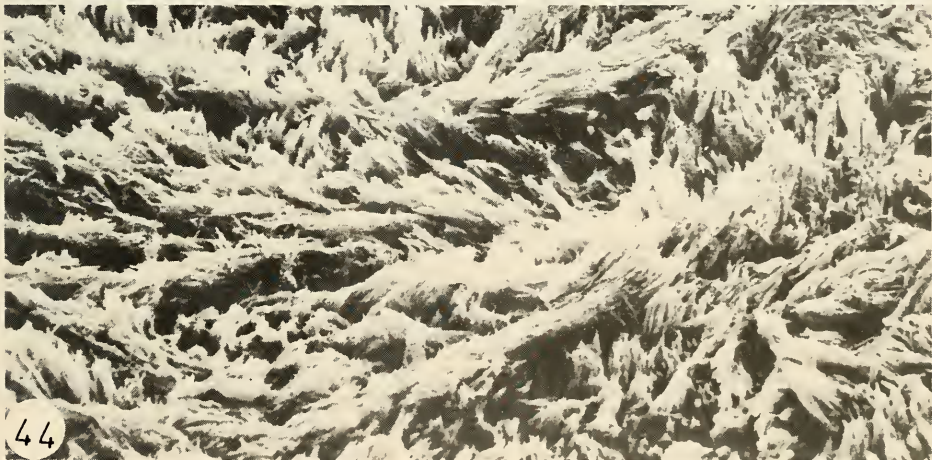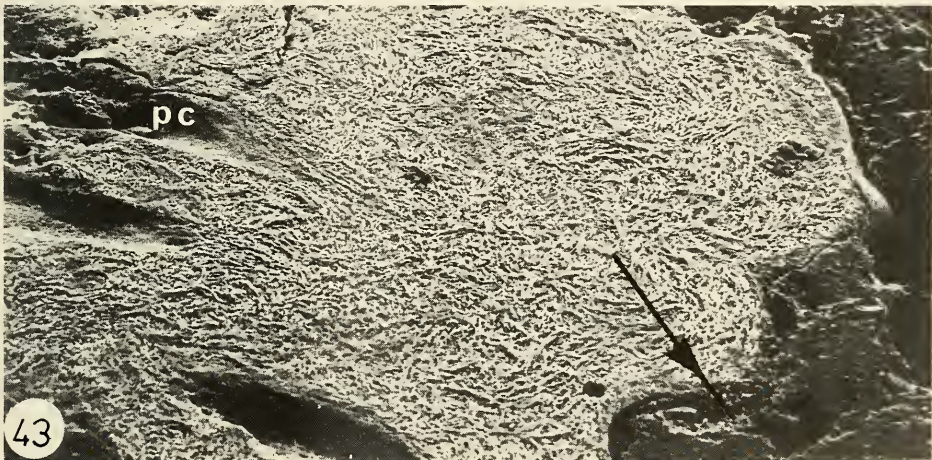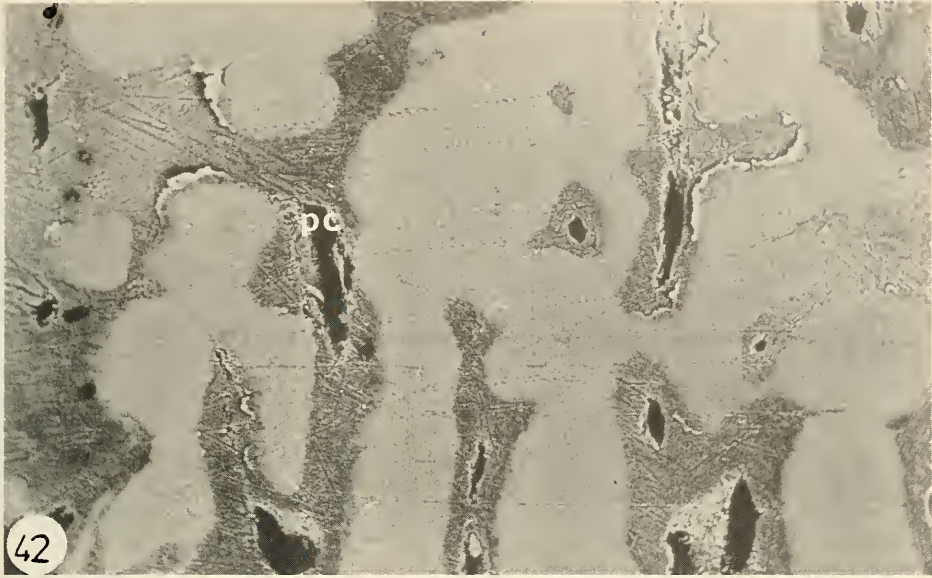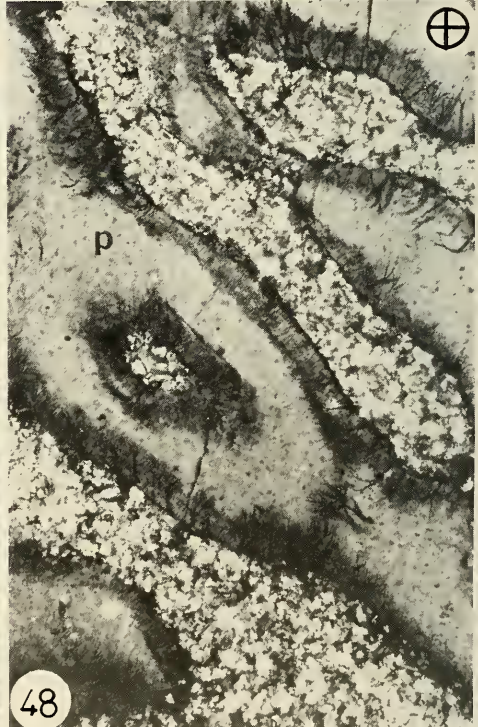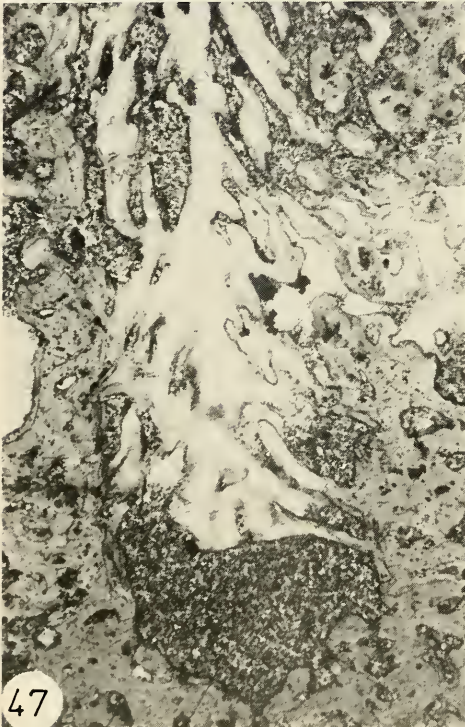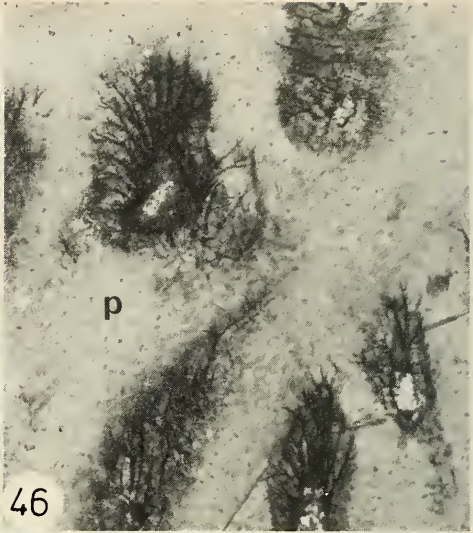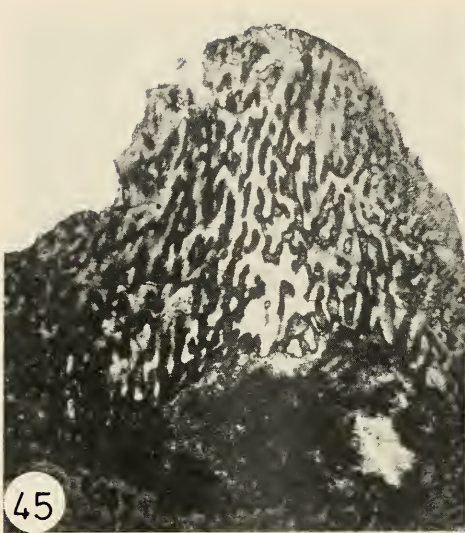
Figs 45-48. Sagenodus inaequalis Owen P7326 & P3381, BM(NH). Carboniferous (fig. 1, pl. 2 & fig. 3, pl. 1, White, 1966, LP Plan).
Fig. 45. Vertical section through anterior cusp of upper tooth plate, irregular arrangement of pulp canals and translucent petrodentine. Field width 52 mm. *Fig. 46.* ½ PL of pulp canals near tritural surface with multibranched tubules emerging from pulp canal into petrodentine. Field width 0.4 mm. *Fig. 47.* Vertical, antero-posterior section through upper tooth plate; one column of petrodentine with many pulp canals beneath one ridge, small pulp chamber. Field width — 35 μm. *Fig. 48.* ½ PL of pulp canals in central region and lining of c.p.d. distinct from petrodentine. Field width — 0.4 mm.
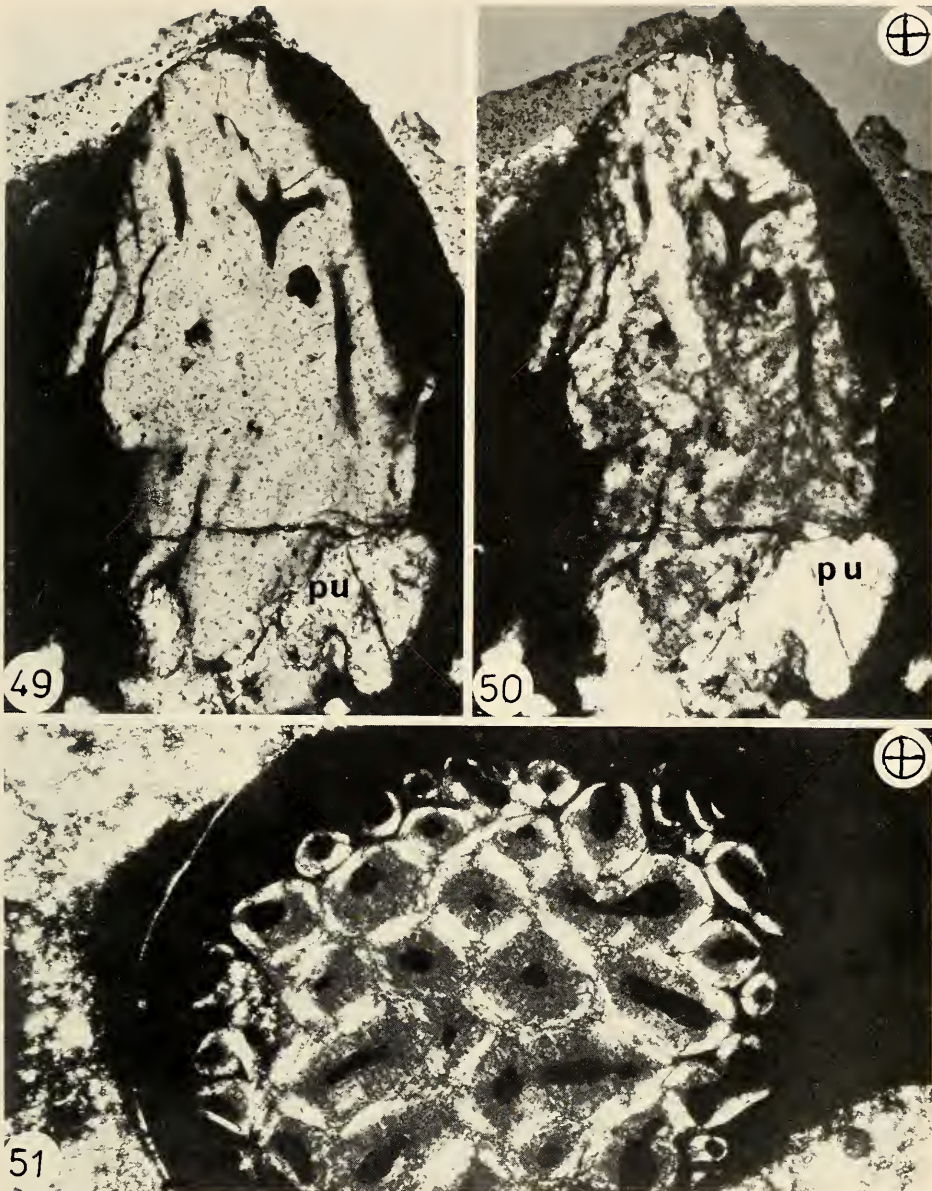
Figs 49-51. Dipterus valenciennesi S & M P44671, P535373 BM(NH). Middle Devonian (fig. 2, pl. 1, LP Plan, White, 1966).
Figs 49, 50. Vertical section through one denticle of upper tooth plate in O.L. and P.L. to show translucency and birefringence of petrodentine. Small pulp chamber separates petrodentine from bone. Irregular arrangement of pulp canals through the petrodentine. Field width 0.6 mm. *Fig. 51.* Horizontal section through one denticle P.L. shows birefringent bands of opposite sign in tissue between the dentine adjacent to pulp canals. Translucency and arrangement of crystal-fibre bundles indicative of petrodentine. Field width 1.2 mm.

Petrodentine differs from trabecular dentine by its extreme hardness which results from high levels of mineralization and reduction of organic matrix. Its production by specialist cells at the pulp surface (whether a pulp chamber or a pulp canal) in a relatively continuous sequence of growth makes petrodentine a unique tissue. The microstructure of mature petrodentine, with domains in which relatively large crystals are grouped in parallel bundles but tubules housing odontoblast cell processes are absent, is very similar to enameloid or acrodin in the separate teeth of elasmobranchs and actinopterygians. However the production of these tissues is entirely different and, therefore, they are considered not to be homologous. In dipnoans a specialist cell population has developed from a presumed single population of dentine-producing cells of the mesodermal dental pulp. Studies of larval tooth plates show that petrodentine is produced by a distinct group of cells from those producing the outermost, primary dentine. Petrodentine forms in this way in the smallest separate denticles which fuse together to make the radiate ridges of the tooth plate. It is beyond the scope of this paper to discuss whether the specialist cells, petroblasts, are derived from one or two populations of progenitor cells, or by dedifferentiation of odontoblast cells. However, some petrodentine surfaces are subsequently lined by dentine with tubules, and circumstantial evidence suggests that some petroblasts revert to odontoblasts in these regions of slower growth, although adjacent cells continue to form thicker petrodentine. Details of the formation, development and growth of petrodentine are not known. Kemp (1979) has stated that petrodentine (central material) does not stain for collagen and that it does not become hypermineralized as a result of loss of collagen. She has suggested that fine reticulin fibres may be the basis of this tissue matrix. Clearly agreement can only be reached when more information is available at the ultrastructural or biochemical level. It is generally stated that fine tubules from the odontoblast cells do not remain in the petrodentine. However, during the first stage of its production there are cell process spaces. These are probably polarized cell processes temporarily trapped in the first formed secretion. Cell processes withdraw as more petrodentine is secreted and the first-formed tissue becomes completely calcified throughout. It will be interesting to know whether the cell process controls the orientation of the crystals or whether the type of organic matrix is the controlling factor.

Some of the Carboniferous forms examined, for example *Sagenodus,* have very irregular arrangements of the pulp canals but it is concluded that the tissue between them in the central part of the ridges is probably petrodentine. *Scaumenacia* also has petrodentine (Ørvig, 1983, pers. comm.) dispersed between numerous pulp canals. The pattern of change that produced different types of tooth plates is not understood. The arrangement of the tissues in lepidosirenids clearly differs from that in ceratodontids, but whether the arrangement in *Sagenodus* was modified to give either

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Figs 52-56. *Chirodipterus australis* Miles BMR 22592-4, P52561 BM(NH). Middle Devonian.
Fig. 52. P.L. of vertical section through labial margin of lower tooth plate, shows extent of birefringent petrodentine and irregular arrangement of pulp canals. These anastomose and taper markedly from forming surface to tritural surface. Field width — 3.13 mm. *Fig. 53.* S.e.m. of section adjacent to Fig. 52 prepared as polished, etched surface (1NHCl, 30 secs). Fringe of deeper etched material at lower border where petrodentine is forming and is less highly mineralized. Field width — 1.8 mm. *Fig. 54.* S.e.m. of worn tritural surface etched to show difference between petrodentine and c.p.d. around pulp canals. Many small tubules throughout petrodentine. Field width — 60 μm. *Fig. 55.* S.e.m. of field from Fig. 53, interwoven matrix between pulp canals, many small tubules between crystal-fibre bundles. Field width — 180 μm. *Fig. 56.* S.e.m. at higher magnification of petrodentine to show separate crystals in random arrangement, although some lie in parallel groups. Field width — 25 μm.
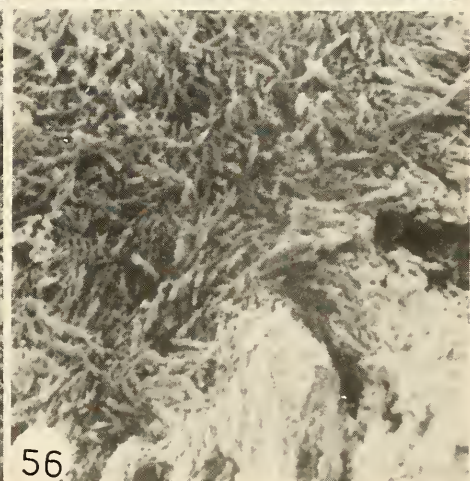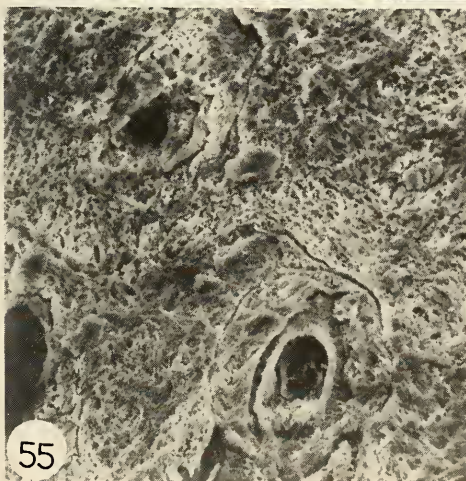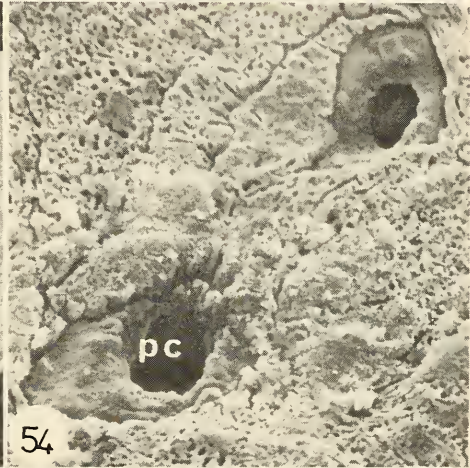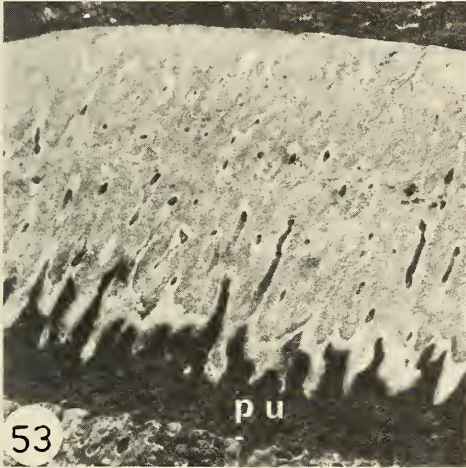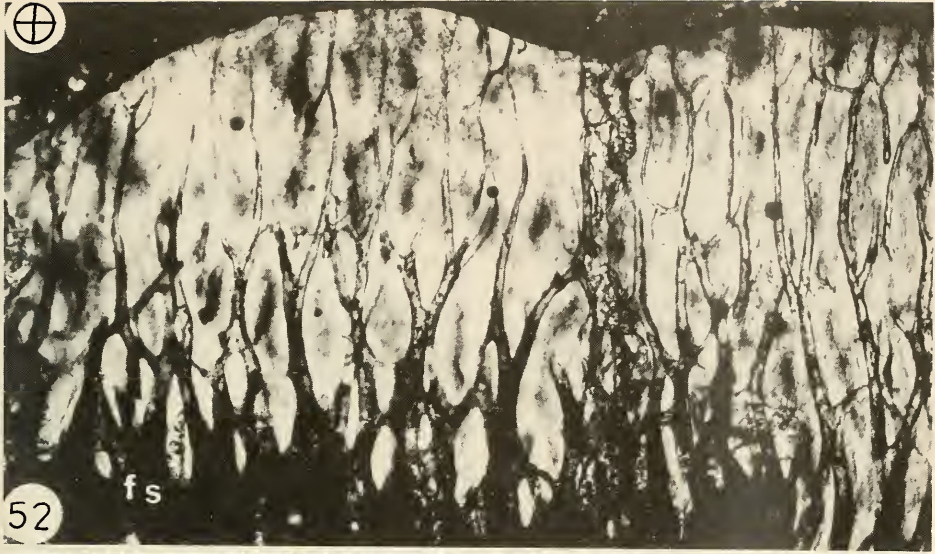
Neoceratodus forsteri   Ceratodus madagascariensis
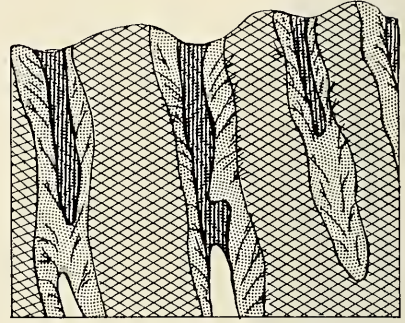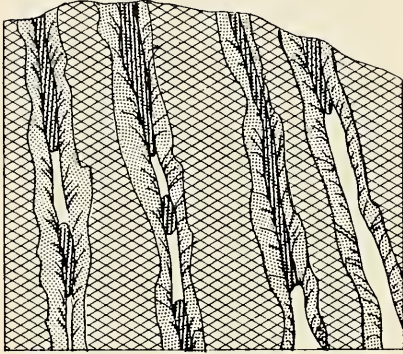
Protopterus aethiopicus   Lepidosiren paradoxa
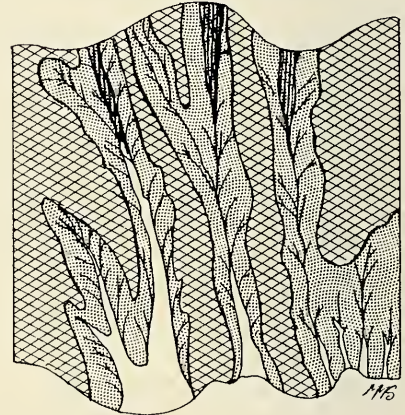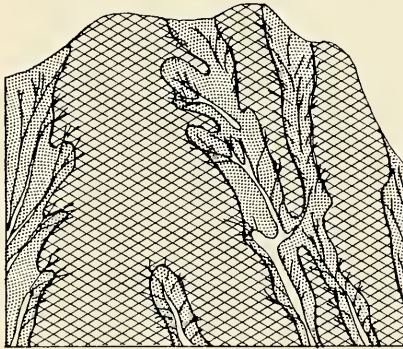
200μm

Fig. 57. Each area represents the arrangement of tissues immediately beneath a worn region of the tritural surface. Only in *Lepidosiren* is the formative surface also included (same section as Figs 16, 17). In this region the pulp canals are almost parallel as in the two ceratodontids. The section of *Protopterus* is through the main part of ridge two and is typical of what is called a 'column of petrodentine', as shown in Fig. 6. *Neoceratodus* is from a decalcified section and that of *Ceratodus* from a ground section. The key is the same as Fig. 1 with the addition of vertical-line hatching for infilling dentine in each pulp canal.

type has not been determined. The tooth plates of *Monongahela,* also with petrodentine, are most interesting and together with those of *Gnathorhiza* merit further study.

The term 'columns of petrodentine' has been used to describe the peculiar arrangement of petrodentine in lepidosirenids but it could equally well be applied to the structure in *Sagenodus* or *Dipterus,* except that more vascular canals are found within their petrodentine. It is difficult, therefore, to decide if this is an advanced character, particularly as in some regions of the tooth plate of *Lepidosiren* petrodentine is not arranged as columns but as an extensive region with parallel, vertical pulp canals. A comparison of the proportion of petrodentine to dentine around the pulp canals is made in Fig. 57 where four examples taken close to the tritural surfaces are illustrated.

Growth lines have been identified in many of the fossil forms and these are a guide to both the areas of growth and to the direction of growth. These topics will be pursued in subsequent publications together with the pattern of growth that is established in larval tooth plates and continued into the adult stages (Smith, 1984).

Petrodentine is a feature of tooth plates in genera as old as Middle Devonian but it has not been shown to be present in genera without tooth plates. This question should be investigated using the criteria developed in this paper. If triturating dentitions define a line of evolution as proposed by Campbell and Barwick (1983), then it is important to know if petrodentine is found exclusively in these forms. We also need to know if petrodentine is present in the most primitive representatives of dipnoans such as *Dipnorhynchus sussmilchi* (Etheridge) and *Speonesydrion iani* Campbell and Barwick. Preliminary observations by Smith and Campbell suggest that it is not.

Whether petrodentine occurs in other gnathostomes has not been considered herein. Ørvig (1976, 1983 MS) has described this growth of pleromin in holocephalan tooth plates, producing tritural columns within the plate. There appear to be many similarities with dipnoan tissues; but whether this is indicative of a close relationship between the groups is not possible to decide at present. This may be an example of a convergent specialization but without proper analysis of all the characters of holocephalan dentitions the question must remain open. Kemp (1984) has published some new material to compare the histological structure and growth pattern of tooth plates of *Neoceratodus forsteri* and *Callorhynchus milii*. From this she has concluded that they share a similar growth pattern.

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KEY TO ABBREVIATIONS

b   — bone

d   — dentine

cp.d   — circumpulpal dentine

e   — enamel

g.l.   — growth line

f.s.   — forming surface

M   — medial

od   — odontoblast

p   — petrodentine

1°   — primary

p.c.   — pulp canal

pe   — petroblast

pu   — pulp cavity

r   — resorption surface

t   — tubules

t.s   — tritural surface

Ph   — phase contrast

P.L. — polarized light

O.L. — ordinary light

Specimen location — BM (NH) British Museum (Natural History); IMGP — Institute and Museum of Geology and Palaeontology, Tübingen; BMR — Bureau of Mineral Resources, Canberra; FM — Field Museum of Natural History, Chicago. WJ — Warwick James collection, Royal Dental Hospital, London.